Climatic Sensitivity and Growth of Southern Temperate Trees in the Eastern US: Implications for the Carbon Cycle

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ABSTRACT

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Climatic warming over the past 200 years is expected to accelerate over the next century. Such a change will have significant impacts on forest composition, species ranges and the terrestrial carbon pool. Forecasts of the impact of future climate on temperate, eastern North America forests, however, vary widely. The range of forecasts is primarily related to the paucity of data on the climate sensitivity of most tree species. Tree-ring analysis gives the opportunity to explore the long-term relationship between climate and tree growth as well as long-term growth trends. Three tree-ring based networks comprised of seven southern-temperate tree species covering over more than 400,000 km^2 in the eastern U.S. were created to study the response of radial growth to climate and growth rates of these species. Winter temperatures were found to be a significant factor limiting growth of most species, with Atlantic white-cedar (*Chameacyparis thyoides*) being the most limited. Individual species' temperature response differed the most during the dormant seasons, which could be biologically important. Geography plays an important role in the climatic response of species. Growth rates of the northern red oak (*Quercus rubra*) in the forest surrounding the Harvard Forest eddy-flux tower are among the lowest of 20 populations studied across the northeastern U.S., which suggests other northern red oak-dominated forests may be sequestering significantly more atmospheric CO_2 than previously thought. Tree age does not appear to

limit individual-tree growth rates of white oak (*Q. alba*), chestnut oak (*Q. alba*), yellow-poplar (*Liriodendron tulipifera*) and northern red oak. In fact, growth rates for these species and Atlantic white-cedar have accelerated over the last 50-150 years. Although accelerated tree growth rates are not proportional to increased productivity at the stand or ecosystem level, these results suggest that old trees and forests can be an important element of the carbon cycle. Results here on a small number of the tree species in the eastern U.S. suggest that there is much to learn on the impact of climate on tree growth and climate response and that there are still large uncertainties on how forested ecosystems will respond to future climate change.

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Acknowledgements

The research presented here dissertation only has one name on the cover. This, however, is misleading. There is no way the research would have been completed without a seven-nation army. I am extremely fortunate to have had a great group of people pushing, pulling, inspiring and supporting me throughout this process. I cannot possibly thank everyone who assisted me. I encourage all to check out Chapters 2 and 4 as well as Appendices A and C for a more complete list. Appendix C is important. It lists the 53 people who volunteered for fieldwork. I am indebted to each person. For those I might have forgotten in this and other sections [and this pains me if it is true], I am sorry.

There are a few that I would like to single out, in no particular order, for going above and beyond, so to speak. Ned Barnard has been great by helping me make contacts with NYC Parks for getting permission to core, being a driver on a couple epic road trips, regularly volunteering for dull lab work [core prep, sorting, etc.] and being a good confidant and supporter. Myvonwynn Hopton played multiple roles in support of this research and my development from a student to, eventually, faculty member: technician, volunteer field help, colleague, advisee. Her dedication, principled nature and open-mindedness are inspiring. I have to thank Erika Mashig for her help at the beginning of this project; a period where I wasn't exactly sure what I was doing. Her first trip as a member of our lab was to core some of the hardest trees in the eastern U.S. Yet, she never complained or quit and continued to volunteer when possible. Likewise, Kevin Vranes and Dave Frank were always willing to do fieldwork at a moment's notice. Their help during some physically grueling days was characterized by joy and enthusiasm even though it wasn't their research. This made my work much, much easier. Finally, I need to thanks J. Morgan Varner, III. His support through his roles as a friend and colleague over the years as well as many inspiring and harassing phone calls made knocking this thing out at the end more than bearable.

Other friends and family to thank: the extended Pederson clan [Ma, Pa, John Lawton, Erica, Kathryn, Derek, among many others]; the Cabaniss' [Cabanii?], especially the late Dr. Daniel Cabaniss for showing me that hard work is noble; Dee and Calla for being playful and loving diversions of the constant grind.

I need to acknowledge the scientific/academic pedigree that inspired, taught and guided me along this winding road. In chronological order [what would you expect from someone who works with time-series?]: Dr. Shirley Crawford at Morrisville Ag & Tech junior college who told me to go into a more vigorous program than the environmental sciences as I was changing my major. She was right and I continue to pass her advice along; Drs. Don Leopold and Robin Kimmerer at SUNY-College of Environmental Science and Forestry whose incredible teaching styles made me the complete tree geek that I am; Dr. Charlie Hall, whose teaching style and eye for the future of hot ecological topics goes unrivaled. Most importantly, I will never forget him saying that I was not too bad for a simple country boy; Dr Bob Jones, then at Auburn University, for taking on a fellow stumpy and giving me the opportunity to study old-growth and forest ecology when I was initially sure it wasn't possible in the forestry department at Auburn; Dr. Becky Shartiz, of the Savannah River Ecological Laboratory, whose warm and rigorous advising style helped get me through some tough times and into Columbia. Her style is one I continue to strive for.; Dr. David Orwig of the Harvard Forest, whose been a critical colleague to bounce ideas off of and, more importantly, a good friend; The entire staff and post-docs of the Tree-Ring Lab of Lamont-Doherty Earth Observatory. You've helped lift this country boy to a level not thought possible; Dr. Gordon Jacoby, whose patient guidance and support helped me believe I could be a successful student here; Dr. Dorothy Peteet whose enthusiasm is so durn infectious that I seriously considering doing a pollen study on top of my tree-ring study! Dorothy was also instrumental in getting me into this program – thanks Dorothy!; Dr. Kevin Griffin, my academic advisor, who said, "If it helps you for me to not be involved in your dissertation work, then I will stay out of the way. And, if it helps you for me to be involved, then I'll stay involved." IT was exactly what I wanted to hear. Most importantly, he kept his word and really helped when I needed it, like when he read v. 0.8 of this dissertation over the course of one weekend!; Dr. Ed Cook whose blowtorch has taken off some rough edges. Seriously, Ed has been a great part of my development.

I need to thank my financial pedigree. First, I want to thank Dorothy Peteet and Jim Hansen for helping secure a NASA Fellowship. Most importantly, many thanks to Christa Farmer about letting me in on the wonderful, but not well known Department of Energy Global Change Education Fellowship Program. Christa, you saved me. Seriously. Thanks to Jeff Gaffney, Milt Constantin and Mary Kinney for running a warm and homey fellowship program while fighting the ills of budget constraints. This has been the primary funding source for this dissertation. Many, many thanks.

As our society has become environmentally aware, it has gotten more difficult to get permission to core trees. I've acknowledged these people throughout the dissertation. There are a few that need special thanks because they understand that there is not a

contradiction between the coring of trees and protection of the environment. I need to thank Tad Norton, formerly of the NYS Department of Environmental Conservation, for helping to navigate my applications through the lengthy and bureaucratic NYS government permitting process. Special thanks to The Nature Conservancy, who to my surprise, were very open to tree-ring research. Two people of TNC deserve special attention: Nancy Sferra of the Maine chapter of The Nature Conservancy for letting Myvowynn Hopton and I permission to sample in some very special places. And finally, many, many thanks to Tim Tear for not only giving me permission to conduct research in many preserves of the eastern NY chapter of The Nature Conservancy, but reaching out to people in other chapters to let them know this was useful research. He opened many doors and made my life so much easier. Thanks Tim!

There are no acknowledgements in Chapter 3 as it is the only research chapter not submitted for publication or published. So, let me thank people involved in this work here; it was this project that helped fund much of the dissertation, so it is appropriate that they be thanked up front: Many thanks to Dr. Steve Wofsy, Elizabeth Hammond Pyle, Scott Seleska and David Bryant of Harvard University [at the time of this research] and Audrey Barker-Plotkin, David Foster and the staff at the Harvard Forest for support. I need to thank Tom Singer of Singer Farms in Appleton, NY; The Central and Western Chapter of The Nature Conservancy; Peter Smallidge and Cornell University; Bruce Gilman of Finger Lakes Community College; Peter Blue of Oneonta University; Sean Fagan; Mike Curley, Rich McDermott, Rick Fenton, Ron Cadieux, Steve Warne, Tad Norton, Tom Martin, and Gary Pratt of the NYS Department of Environmental Conservation; Bill Schuster of Black Rock Forest; Sarah Price and Lucy Kuriger of

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Dedication

This dissertation is dedicated to my grandfather, Phillip Monforte. Although you probably wouldn't find these accomplishments through Google, he accomplished much over his life with an 8th-grade education. I thank him for taking a risk by leaving Sicily to see the world and then settling in central New York State. His adventuresome spirit was passed to me during the many summer days I spent working on his farm and visiting with his farmer friends in the area. He presented me with many life lessons during those days; some intentional, some not. They are lessons I hold on to and try to pass along.

Chapter 1: Rationale for Dissertation Research and Dissertation Layout

Rationale for Dissertation Research:

An increase in atmospheric greenhouse gas concentrations is forecast to induce a rapid climate change over the next 100 years. Associated with predicted warming of annual global temperatures from 1.4 to 5.8°C are an increase in total precipitation, increased annual variability of precipitation and more frequent extreme weather events (IPCC, 2001). The uncertainty in the amount of future warming, however, has been reduced. In fact, it seems highly likely that future warming is expected to be greater than what has occurred over that last 100 years (Meehl et al., 2005). A change in climate such as this will alter the competition between species, which would lead to changes in ecosystem productivity and composition in eastern U.S. forests.

Forecasts of the impact of climate change on eastern U.S. forests ranges from a negligible change in species composition to a rapid shift in species distributions to a significant dieback and mortality of certain species (*e.g.* Solomon, 1986; Pastor and Post, 1988; Overpeck et al., 1991; Iverson and Prasad, 1998; Loehle, 2000; Bachelet et al., 2001; IPCC 2001). One reason for the wide range of forecasts is the limited amount of data on climate response of most species (Loehle and LeBlanc, 1996; Schenk, 1996). The data that exist is based on: 1) seedling or saplings, 2) short-term in length or 3) limited in understanding decadal scale changes in climate or climate variability. Most information on mature tree sensitivity to climate is limited to classic dendroclimatological sites (xeric locations, grassland ecotones or treelines) or a few number of species. (*e.g.* Botkin et al., 1972; Shugart, 1984; Bartlein et al., 1986; Solomon, 1986; Cook and Cole, 1991;

Prentice et al., 1991; Pacala and Hurtt, 1993; Loehle and LeBlanc, 1996; Schenk, 1996; Bugman, 2001). In regions with high species diversity or threatened ecosystems like the eastern U.S. (Braun, 1950; Laderman, 1989; Noss, 1989), it is critical to understand the influence of climate on species and ecosystems to better anticipate the impact of future climate change.

Paleoecological studies in the eastern U.S. have shown how climate and rapid climate change alter tree distributions and forest composition (Whitehead, 1979; Davis et al., 1980; Gajewski, 1987; Peteet, et al., 1990; Jackson and Whitehead, 1991; Spear et al., 1994; Peteet, 1995; Maenza-Gmelch, 1997; Gajewski, 1998; Kneller and Peteet, 1999; Schauffler and Jacobson, 2002; Shuman et al., 2002). This type of evidence, however, has a limited ability to reveal the mechanisms that alter forest composition. For example, macrofossil evidence indicates that a rise in temperatures of 3 - 4°C in less than 100 years during the Younger Dryas was associated with a dieback of several boreal taxa (*e.g. Picea, Abies, Larix,* paper birch (*Betula papyrifera*)) and replacement by temperate taxa (*Quercus* and *Pinus strobus*) in the lower Hudson Valley and southern New England (Peteet at al., 1990; Peteet, 1995). In contrast to this macrofossil evidence, low levels of boreal tree pollen, perhaps as a result of long-distance wind transport of pollen, suggest that mature trees may have persisted following the Younger-Dryas warming event. Regardless, it is unclear whether rapid warming induced tree mortality or if it intensified drought (*i.e.,* Webb et al., 1993). Therefore, it is important to determine the climatic response of species at annual to centennial time-scales to help improve vegetation models and gain further insight of changes in past vegetation.

Climate has changed significantly over the last 200 years. The 20th century was one of the warmest centuries of the last 500-1000 years while the 19th century was one of the coldest (Mann et al., 1998; Villalba et al., 2003; Cook et al., 2004; Moberg et al., 2005). Changes in the biological systems of the Arctic and high latitudes have been well documented in association with this reversal of global temperatures (*e.g.,* ACIA, 2005). Likewise, changes have been documented in the phenology of species and animal migrations in the mid-latitudes (Bradley et al., 1999; Inouye et al., 2000; Schwartz and Reiter, 2000; Gibbs and Breisch, 2001; Fitter and Fitter, 2002; Primack et al, 2004). Thus, changes in biological systems have been connected to warming over the last century.

Research on the importance of temperature as a factor of tree growth has been focused mostly on high latitude and elevational forests (*e.g.,* Jacoby and D'Arrigo 1989; Briffa, 1992; Becker et al., 1995; Jacoby et al., 1996; Rolland et al, 1998; Briffa et al. 2001; Buckley et al. 1997; Esper et al., 2001; Kullman 2001; McKenzie et al., 2001; Wilmking et al., 2004; Frank and Esper, 2005). In contrast, there have been far fewer studies examining the importance of temperature on tree growth of low-elevation temperate trees, especially in the eastern U.S. (but see Cook and Johnson, 1989; Webb et al., 1993). In fact, the climatic response to temperature change of most trees in the eastern U.S. is unknown (Loehle and LeBlanc. 1996; Schennk, 1996), with three exceptions: eastern hemlock (*Tsuga Canadensis* (L.) Carr.), red spruce (*Picea rubens* Sarg.), and loblolly pine (*Pinus taeda* L.) (Conkey, 1986; Cook et al., 1987; Cook and Cole, 1991; Cook et al., 1998). The lack of temperature studies in this region may be directly due to the fact that drought stress has repeatedly been shown to be a dominant factor of tree growth and forest dynamics (*e.g.,* Douglass, 1920; Schumacher and Day, 1939; Cook and Jacoby, 1977; Currie and Paquin, 1987; Cook, 1991; Stahle and Cleaveland, 1992; Graumlich, 1993; Orwig and Abrams 1997; Pedersen, 1998; Stephenson, 1998; LeBlanc and Terrell, 2001; Cook et al., 1999, 2001). Therefore, it is imperative that the temperature response of eastern U.S. tree species be studied, especially considering that future changes in temperature appear to be better understood than changes in precipitation (IPCC, 2001).

Climate change and it associated effects on tree growth rates have important ramifications for the global carbon cycle (*i.e.,* Myneni et al., 1997; Nemani et al., 2003; Mathews et al., 2005). Temperate regions have some of the largest global aboveground terrestrial carbon pools (Myneni et al. 2001), show the largest increase in forest productivity of global forest types as they age (Pregitzer and Euskirchen, 2004), and have been implicated as an important part of the so-called 'missing carbon sink' of atmospheric CO_2 (e.g., Tans et al., 1990; Keeling et al., 1996; Myneni et al., 1997; Battle et al., 2000). Understanding the factors that govern carbon sequestration in these forests is vital because changes in atmospheric CO_2 concentrations are expected to influence futures changes in climate.

The region of study for my dissertation ranges from Alabama to Michigan to southern Maine (Figure 1). Most of the research is focused around the vegetational ecotone in southern New England and eastern New York State (NE/NY) (Bray, 1915; Braun, 1950; Eyre, 1980; Bailey, 1995). This ecotone coincides with the northern-range-margin of many southern temperate tree species and fauna (Little, 1971; Stewart and Rossi, 1981) as well as a peak in biodiversity in eastern New Your State (NY-GAP,

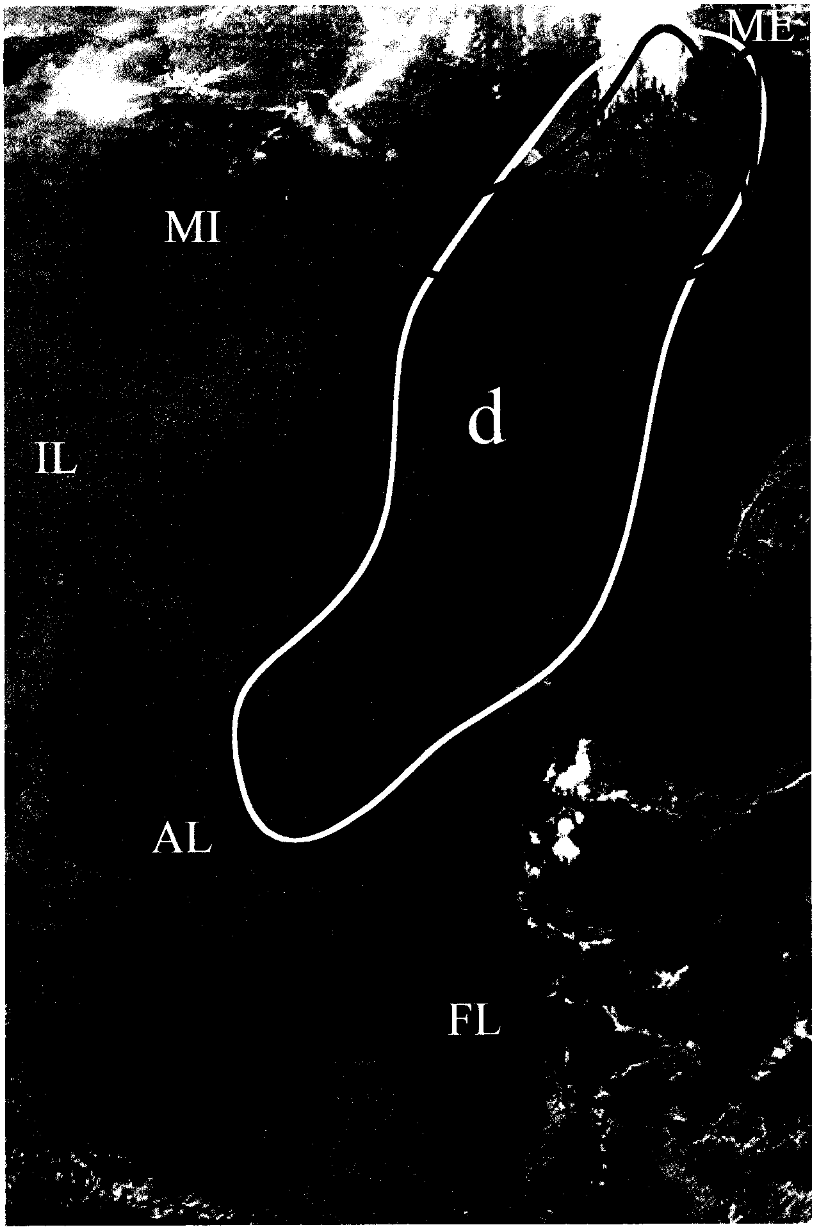

Figure 1 - Spatial Distribution of Dissertation Research and Collection Networks in the Eastern United States. A - Chapter 2: ‘The Influence of Winter Temperatures on the Annual Radial Growth of Six Northern Range Margin Tree Species’, B - Chapter 3: ‘Growth and Climatic Sensitivity of Northern Red Oak in the Northeastern U.S.: Placing Carbon Uptake at the Harvard Forest in a Regional Perspective’, C - Chapter 4:‘Evidence of Accelerated Growth in Old Trees’. a - Appendix A: ‘Climate Sensitivity of Atlantic White Cedar at Its Northern Range Limit’, and d - Appendix D: ‘Table of Tree Species Collections from Georgia to Maine’. Five states in the eastern U.S. bound the geographic distribution of the research carried out during this dissertation. Starting in the west and moving clockwise, these states are: IL - Illinois, MI - Michigan, ME - Maine, FL - Florida and AL - Alabama. Image courtesy of NASA’s Visible Earth program (http://visibleearth.nasa.gov/).

2001) (Figure 2). A southern temperate species here is defined as a species that is more commonly found between 32° and 40° north latitude in the eastern U.S., but rarely north of 45° north latitude. The NE/NY ecotone is one of the few places in eastern North

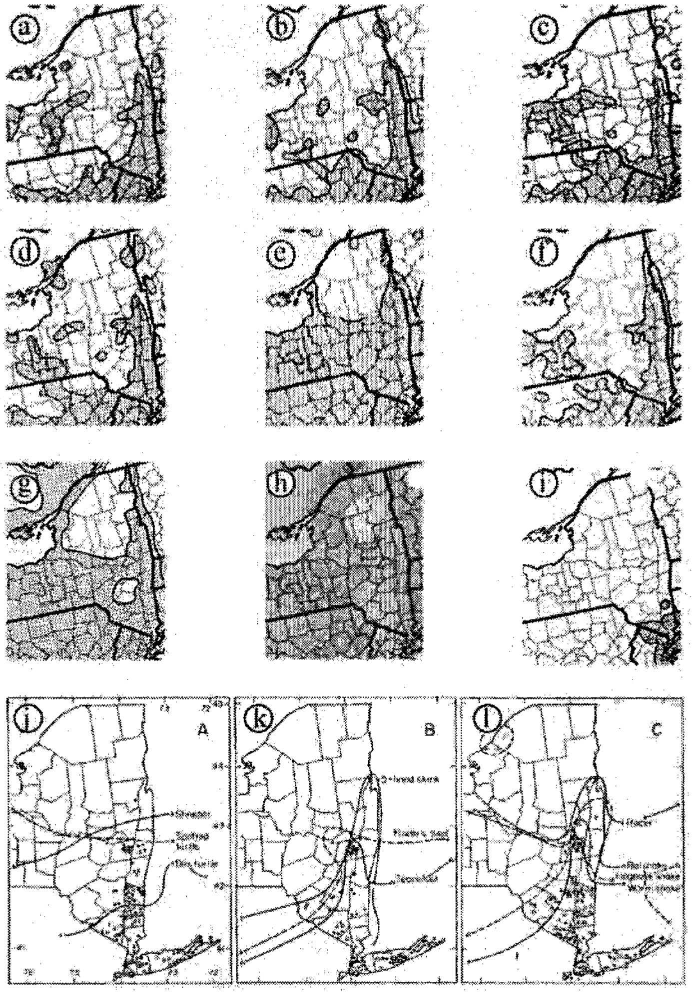

Figure 2 - Distributions of Tree and Faunal Species Where a Northern Range Limit is Found in the Hudson River Valley. a) pignut hickory (*Carya glabra*), b) black oak (*Quercus velutina*), c) yellow-poplar (*Liriodendron tulipifera*), d) pitch pine (*Pinus rigida*), e) black birch (*Betlua lenta*), f) chestnut oak (*Q. prinus*), g) white oak (*Q. alba*), h) northern red oak (*Q. rubra*), i) Atlantic white cedar (*Chameacyparis thyoides*), j) stinkpot (*Sternotherus odoratus*), spotted tuttle (*Clemmys guttata*), and box turtle (*Terrapine carolina*), k) five-lined skink (*Eumeces fasciatus*), Fowler's toad (*Bufo woodhousei fowleri*), eastern spadefoot (*Scaphiopus holbrooki*), and l) racer (*Coluber constrictor*), rat snake (*Elaphe obsoleta*), eastern hognose snake (*Heterodon platyrhinos*) and worm snake (*Carphophis amoenus*). a) - i) adapted from Little (1971). j) - l) adapted from Stewart and Rossi (1981).

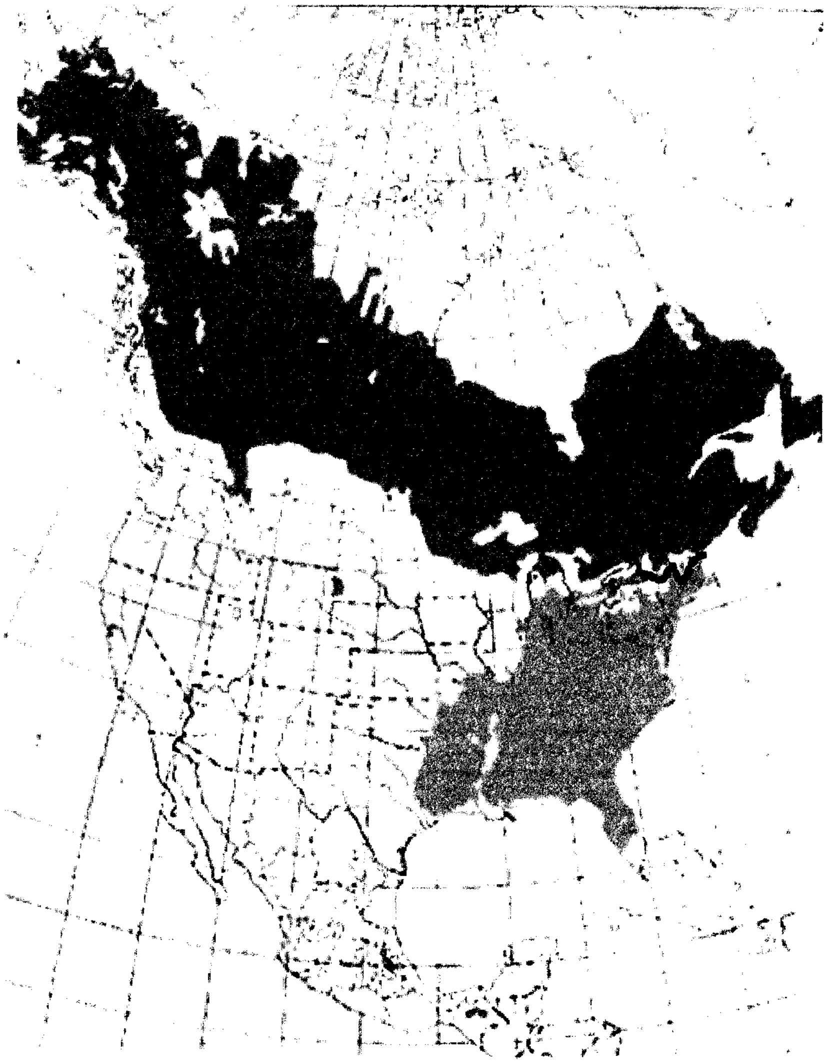

Figure 3: Distribution of White Spruce and Black Tupelo Across North America. The distributions of white spruce (blue) and black tupelo (orange) best represent the New York-New England ecotone (represented by the dashed black line). Figure adapted from Little (1971).

America where distributions of boreal and southern temperate species overlap, as symbolized by the distributions of black tupelo (*Nyssa sylvatica* Marsh.) and white spruce (*Picea glauca* (Moench) Voss) (Figure 3).

This region is ideal for climate change studies for several reasons. First, areas with regional ecotones or a mix of boreal and temperate species are prime areas for understanding the influence of climate change on forested ecosystems because species sensitivity to climate is thought to be strongest in these areas (Solomon, 1986; Neilson, 1993; Risser, 1995; Loehle, 2000; Peteet, 2000). The similarity between the temperature gradient and NE/NY ecotone emphasizes the region's potential sensitivity to temperature (Figure 4). Second, there have been significant changes in hydrological cycles and temperatures over the last century in this region (Karl et al., 1998; DeGaetano and Allen, 2002; Groisman et al., 2004) making it possible to detect the impact of climate change on tree growth. Finally, the northeastern U.S. will potentially have the largest change in temperature within the coterminous US (Currie, 2001), so the need for understanding the temperature sensitivity of tree species is most critical in this region.

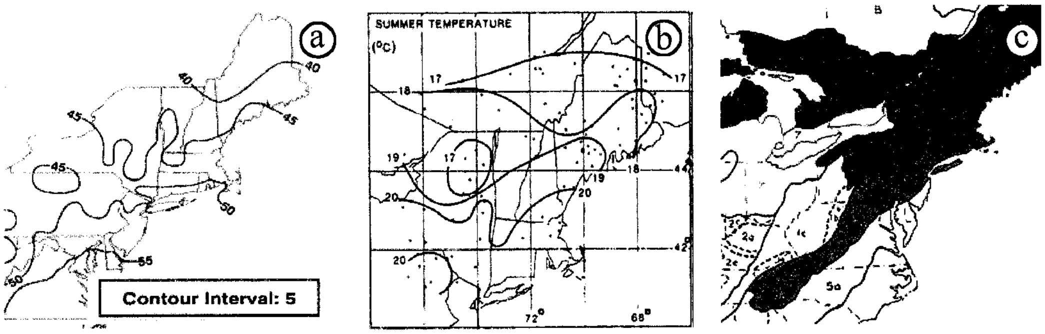

Figure 4 - Similarities Between the Spatial Pattern of a) Annual and b) Summer Temperatures and c) Forest Types. a) adapted from Owenby et al. (2001). b) adapted from Gajewski (1988). c) adapted from Braun (1950). Red in c) represents the spatial distribution of the northern hardwood forest type, which is typified by beech-birch-maple. Yellow in c) represents the spatial distribution of the maple-basswood forest type. Green in c) represents the spatial distribution of the oak-hickory forest type, formerly known as chestnut-oak-hickory.

Dissertation Layout

My dissertation research focuses on three primary questions: 1) "*Is temperature an important factor of southern temperate tree species growth rates*?", 2) "*What are the* *biotic and abiotic factors influencing tree growth rates/carbon uptake*?" and 3) "*Have tree growth rates changed significantly over the past two centuries*?"

The importance of temperature as a growth factor is the focus of Chapter 2: '*The Influence of Winter Temperatures on the Annual Radial Growth of Six Northern-Range-Margin Tree Species'* (Pederson et al., 2004) and Appendix – A: *'Climate Sensitivity of Atlantic White Cedar at Its Northern Range Limit'* (Hopton and Pederson, in press). Its role is also addressed in Chapter 3: *'Growth and Climatic Sensitivity of Northern Red Oak in the Northeastern U.S.: Placing Carbon Uptake at the Harvard Forest in a Regional Perspective'*.

U.S. Forest Service Inventory Data has been the primary data source for studying carbon uptake and sequestration in the eastern U.S. (*e.g.* Caspersen et al., 2000; Goodale et al., 2002; Joos et al., 2002). While this type of data may be adequate for large-scale stand level biomass measurements, the frequent replacement of lost 'permanent plots' and long time intervals between measurements limit the understanding of annual tree growth rates. Annual measurements of carbon sequestration in a northern red oak dominated, mixed hardwood and conifer forest at the Harvard Forest, MA has added roughly 2 tons of carbon ha^{-1} yr^{-1} between 1993 and 2000 (Goulden et al., 1996; Barford et al. 2001), suggesting that eastern U.S. temperate forests are an important component of the terrestrial global carbon cycle. Chapter 3 is the primary chapter focused on the biotic and abiotic factors influencing tree growth rates/carbon uptake, although all chapters and Appendix A address this question.

Changes in tree growth rates over the last two centuries in the eastern U.S. forests have not been studied as intensely as in high latitude or altitude forests (although see

Smith et al., 1990; Cook, 1991; Abrams and Orwig, 1995). Changes in tree growth rates are the focus of Chapter 4: *'Evidence Of Accelerated Growth in Old Trees'* and also addressed in Chapter 3 and Appendix – A. An outgrowth of this question is the analysis of growth rates of old trees. A prevailing assumption is that tree growth rates decline as they age. Analysis of tree growth rates suggest this assumption may not be correct.

This dissertation is laid out in seven sections. Following this chapter, the order is **Chapter 2**: '*The Influence of Winter Temperatures on the Annual Radial Growth of Six Northern-Range-Margin Tree Species'*, **Chapter 3**: *'Growth and Climatic Sensitivity of Northern Red Oak in the Northeastern U.S.: Placing Carbon Uptake at the Harvard Forest in a Regional Perspective'*, **Chapter 4**: *'Evidence Of Accelerated Growth in Old Trees'*, **Chapter 5**: '*Climatic Sensitivity and Growth of Southern Temperate Species in the Eastern U.S.'*, **Appendix A** - *'Climate Sensitivity of Atlantic White Cedar at Its Northern Range Limit'* and **Appendix B** - '*Gypsy Moth Impacts on Tree Growth*', and **Appendix C** - *'Table of Tree-Ring Collections Between 1999 and 2004*'. Chapter 2 is published as Pederson et al. (2004). Appendix A has been accepted for publication (Hopton and Pederson, in press). Appendices B is a short discussion derived from research conducted for Chapter 3. Appendix C is a list of tree-ring collections made during this dissertation independently and with colleagues.

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ORIGINAL ARTICLE

The influence of winter temperatures on the annual radial growth of six northern range margin tree species

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Abstract

This study explores the influence of temperature on the growth of six northern range margin (NRM) tree species in the Hudson River Valley (HRV). The HRV has excellent geographic and floristic qualities to study the influence of climate change on forested ecosystems. Indices of radial growth for three populations per species are developed and correlated against average minimum and maximum monthly temperatures from 1897 to 1994. Only positive correlations to temperature are considered for this analysis. Principal component analysis (PCA) is performed on chronologies over the entire HRV and at four subregions. PCA reveals a strong common signal among populations at subregional and regional scales. January temperatures most limit growth at the ecosystem level, supporting the hypothesis that winter temperatures may control vegetational ecotones. Surprisingly, growth of the oak hickory ecosystem is most limited by January temperatures only in the southern half of the study region. Chestnut and white oak are the primary species driving the geographic pattern. As winter xylem embolism is a constant factor for ring-porous species, snow cover and its interaction on fine root mortality may be the leading factors of the pattern of temperature sensitivity. Species-specific differences in temperature sensitivity are apparent. Atlantic white-cedar (AWC) and pitch pine are more sensitive to the entire winter season (December March) while oak and hickory are most sensitive to January temperatures. AWC is most sensitive species to temperature. Chestnut and white oak in the HRV are more sensitive to winter temperature than red oak. Pignut hickory has the most unique response with significant relations to late growing season temperatures. Interestingly, AWC and pitch pine are sensitive to winter temperatures at their NRM while oak and hickory are not. Our results suggest that temperature limitations of growth may be species and phylogenetically specific. They also indicate that the influence of temperature on radial growth at species and ecosystem levels may operate differently at varying geographic scales. If these results apply broadly to other temperate regions, winter temperatures may play an important role in the terrestrial carbon cycle.

Keywords: Temperature sensitivity; Temperate forests; Geographic temperature response; White oak subgenus; Eastern North America; Oak–hickory ecosystem

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Introduction

It has been forecast that rapid warming over the next 100 years will substantially alter forested ecosystems (Solomon, 1986; Overpeck et al., 1991; Iverson and Prasad, 1998; Bachelet et al., 2001; IPCC, 2001). However, the impact of such warming on ecosystems is uncertain because existing information describing the influence of temperature on growth for most tree species is lacking (Loehle and LeBlanc, 1996). While temperature has been shown to be an important factor of tree growth and forest ecosystem dynamics at treeline (e.g. Jacoby and D'Arrigo, 1989; Villalba, 1994; Briffa et al., 2001; Buckley et al., 1997; Kullman, 2001), it is not as well understood in temperate forests. Because northern range margins (NRM) represent a "species treeline," NRM are optimum locations to determine if temperature limits tree growth in temperate regions. Temperate regions possess some of the largest global aboveground terrestrial carbon pools (Myneni et al., 2001) while also directly providing society with goods and services. Therefore, it is critical to understand the influence of climate change on tree growth in temperate regions.

Radial growth studies of NRM populations indicate that temperature may influence individual species differently. For example, in the southeastern US loblolly pine (*Pinus taeda* L.) growth is positively correlated to winter temperatures only at its NRM locations (Cook et al., 1998). However, eastern hemlock (*Tsuga canadensis* L.) is positively correlated to March temperatures throughout its range in eastern North American (Cook and Cole, 1991). Two mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) populations at high elevation in Alaska are most strongly and positively correlated to March–July temperatures (Wiles et al., 1998). In contrast, a nearby mountain hemlock population at lower elevation has the strongest positive correlation to January–March temperatures (Frank, 1998). An American beech (*Fagus grandifolia* Ehrh.) population near its NRM in eastern Canada is positively correlated to April temperatures (Tardif et al., 2001). These studies show that each species may have a specific temperature response, and therefore, a full understanding of potential changes in forested ecosystems as a result of climatic warming may require the study of many tree species.

We chose six species to investigate the influence of temperature on the radial growth of NRM species in the Hudson River Valley (HRV) (Fig. 1): Atlantic white-cedar (AWC) (*Chamaecyparis thyoides* (L.) B.S.P.), pitch pine (*Pinus rigida* Mill.), chestnut oak (*Quercus prinus* L.), white oak (*Q. alba* L.), northern red oak (*Q. rubra* L.), and pignut hickory (*Carya glabra* Mill.). In general, these species represent the range of distributions for the 30+ NRM species in the HRV (Little, 1971). For

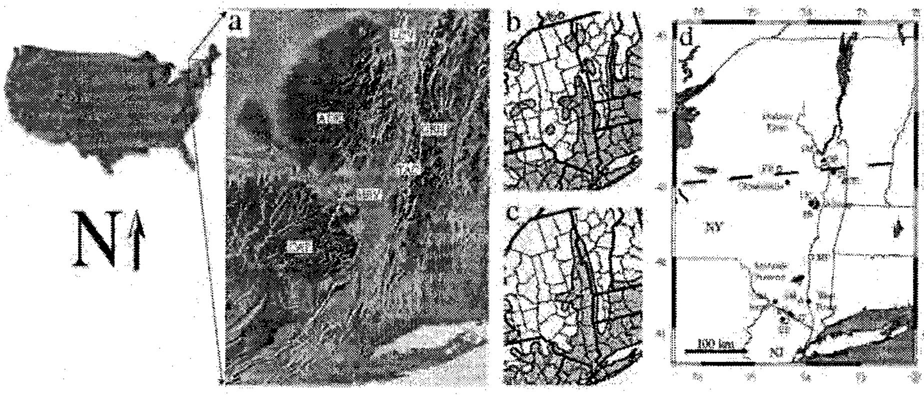

Fig. 1. (a) Topographic map centered on eastern New York State and the Hudson Valley. The darker shades represent mountainous areas and are identified by abbreviations: ADK = Adirondack Mountains; GRN = Green Mountains; TAC = Taconic Mountains; CAT = Catskill Mountains. The two main valleys are designated by: HRV = Hudson River Valley and LCV = Lake Champlain Valley. Distribution maps of (b) pitch pine and (c) chestnut oak. (d) Map of population sites and meteorological stations. Tree species are represented by symbols: (◆) AWC, (▲) pitch pine, (◇) chestnut oak, (△) white oak, (○) red oak, and (■) pignut hickory. Site locations are represented by abbreviations. These populations are (north–south): PM = Prospect Mountain, GF = Glen Lake Fen, RH = Rooster Hill, GE = Goose Egg Ridge, SF = Stott Farm, LK = Lisha Kill, PB = Albany Pine Bush, MP = Montgomery Place, SM = Schunnemunk Mountain, BV = Bellvale Mountain, ST = Sterling Forest, and UB = Uttertown Bog. Meteorological stations are in bold italic and represented by (●). The (- - -) represents the average position of the average location of the convergence of winter Arctic and Pacific Frontal Zones (adapted from Bryson et al., 1970). (a) Adapted from Ray Steiner's Colorlandform Atlas of the United States: http://fermi.jhuapl.edu/states/states.html. (b,c) Adapted from Little (1971).

example, AWC distribution is limited to the southern HRV. Distributions of pitch pine, chestnut oak and pignut hickory are primarily confined to the HRV with outlier populations extending into the Lake Champlain Valley (Figs. 1b and c). Northern red and white oak is distributed northward through the Champlain Valley and into the St. Lawrence River valley. However, both species have range margins along the edges of the Adirondack and Green Mountains.

Geographic, climatic and floristic qualities of the HRV and surrounding mountains make it an excellent region to study climate change and forested ecosystems. Despite varying objectives and methods, different geographic studies of vegetation consistently show a distinct boundary at the northern end of the HRV (Bray, 1915; Braun, 1950; Eyre, 1980; Bailey, 1995; Lugo et al., 1999). Two recent reconstructions of northeastern US vegetation patterns using different methods indicate that this ecotone has been present since European settlement (Russell and Davis, 2001; Cogbill et al., 2002). Further, similarity between the spatial distribution of tree species (Little, 1971) and temperature (Fig. 2 in Gajewski, 1988) suggests the regional ecotone may be related to a temperature gradient. Regional ecotones are prime areas of study for understanding the influence of climate change on forested ecosystems (Solomon, 1986; Neilson, 1993; Risser, 1995; Loehle, 2000; Peteet, 2000).

The purpose of this study is to explore the limitation of temperature on radial growth of NRM tree populations in the HRV. We are focusing on temperature because it may be the best-forecast variable of future climate change (IPCC, 2001) and yet may be the least understood factor of tree growth. Water stress is a well-established and well-understood factor in tree growth and forested ecosystems (e.g. Douglass, 1920; Schumacher and Day, 1939; Fritts, 1965; Cook and Jacoby, 1977; Currie and Paquin, 1987; Cook, 1991; Stahle and Cleaveland, 1992; Graumlich, 1993; Orwig and Abrams, 1997; Pedersen, 1998; Stephenson, 1998; Allen and Breshears, 1998; LeBlanc and Terrell, 2001; Cook et al., 1999, 2001). Specifically, we address the following questions: "Does temperature limit the annual radial growth of NRM species?" and "Do winter temperatures limit growth more than growing season temperatures?"

We will focus only on a positive relationship between temperature and growth because a negative correlation to temperature is often related to water stress (Fritts, 1976; Kramer and Kozlowski, 1979). We will compare species to discern if there is a species-specific temperature response. Principal component analysis (PCA) will offer insights into an ecosystem-level temperature response. While the study species do not represent a specific ecosystem, they represent the northern range limit of a southern temperate forest at the regional scale. Previous studies have shown that the temperature response of different species have distinct geographic patterns (Cook and Cole, 1991; Cook et al., 1998; Hofgaard et al., 1999; Gedalof and Smith, 2001; Peterson and Peterson, 2001). Therefore, we will examine temperature responses at the species and ecosystem levels to determine if a geographic pattern exists in the HRV.

Methods

Region of study

The region of study under investigation is centered on the HRV, extending from northern New Jersey to the southern Adirondack Mountains, northwestern Taconic Mountains and southern Champlain Valley. The Catskill Mountains bound the HRV on the west while the Taconic Mountains bound it on the east. The valley is a half-graben formed during the rifting of the North American and African continents prior to formation of the Atlantic Ocean roughly 220 million years ago. The HRV is a classic fjord because its southern end is below sea level. It also represents a northern extension of the Valley and Ridge Provenance (Brouillet and Whetstone, 1993). The valley's structure and connection to the ocean allows northward penetration of warm, maritime air creating a nearly uniform climate. However, a temperature gradient is produced by the juxtaposition of the low lying, broad valley and mountain formations to the north. Also, the average winter convergence of the winter Arctic and Pacific Frontal Zones coincides with the northern end of the HRV (Bryson et al., 1970). Together, geography and circulation patterns help to create the boundary between a permanently humid climate with warm summers to the south and a cool temperate, subcontinental climate to the north (Brouillet and Whetstone, 1993).

HRV flora and fauna distributions may be related to its geographic and climatic patterns. Many southern tree and herpetological species distributions generally conform to the low-lying portion of the HRV (Little, 1971; Stewart and Rossi, 1981; Smith et al., 2001). Convergence of biotic and abiotic factors has likely made it rich in ecosystem and biological diversity (Lynn and Karlin, 1985; Currie and Paquin, 1987; Thorne, 1993; Smith et al., 2001). The HRV was hypothesized to be a corridor for tree migration into the Adirondack Mountains (Whitehead and Jackson, 1990). This can be inferred by the presence of higher percentages of pollen of southern species further north in the HRV region than surrounding regions throughout the Holocene (Gaudreau and Webb, 1985; Gaudreau, 1986). Should significant future warming occur, high HRV diversity may make it a primary source of species migration to the Adirondack, Catskill, Taconic and Green Mountains.

The number of days when the air temperature is above freezing ranges from 120 to 140 days in the north to 160 180 days in the south in our study region (McNab and Avers, 1994). This is reflected in the first-leaf phenology of lilac (*Syringa chinensis* Willd.). First leaf for lilac is nearly 20 days later in the Adirondack Mountains than in northern New Jersey (Eastern North American Phenology Network, 2003). Total annual precipitation ranges from 865 mm in the north to 1350 mm in the south (NOAA, 1994).

Site selection and descriptions

Three populations per species were sampled throughout the HRV (Fig. 1; Table 1). Sites were selected to at least cover the northern-half of the region, except for AWC. Forests were chosen on the potential for individual trees to be at least 80 120 years old. Secondary considerations of forest selection were trees growing on relatively productive sites with little stand-scale disturbance. No forest met all site preferences. Land-use patterns in the HRV often result in older trees being left on shallower, less productive soils (Glitzenstein et al., 1990). Loss of the American chestnut (*Castanea dentata* L.) in the early 20th century and the current decline of eastern hemlock severely impacted several sites.

The presence of boreal and southern temperate species in a few stands exemplifies the unusual floristics of the region (Table 1). For example, Sterling Forest AWC grows with spruce (*Picea* spp.). Black spruce (*P. mariana* (Mill.) B.S.P.) and eastern larch (*Larix laricina* (Du Roi) K. Koch) grow alongside AWC at Uttertown Bog (Lynn and Karlin, 1985). Northern red oak on Rooster Hill grows with two boreal species, red spruce (*P. rubens* Sarg.) and paper birch (*Betula papyrifera* Marsh.). Nearly one-half of the basal area on the upper, northern slope was red spruce (N. Pederson unpublished data). The canopy of Mohonk Preserve pignut hickory stand is exceptionally diverse considering its northerly latitude. Species composition is evenly distributed among 11 species making it like a mixed-mesophytic forest. However, it is best placed in the Appalachian Oak category since it lacks *Aesculus* spp. (Kuchler, 1964).

Field methods

Healthy appearing, dominant and co-dominant trees were selected for coring to minimize the influence of competition and disturbance on growth. Cores were extracted using a 5.15-mm diameter increment borer. Data presented here are a part of a larger-scale study in which tradeoffs were made between spatial and sample replication where spatial stand replication was considered more valuable than sample replication. Target replication was 16 20 trees per species. A second core was taken from at least one-third of cored trees. Sampling additional trees reduces the standard error of the final chronology more efficiently than increasing the number of cores per tree (Fritts, 1976). The first core was removed perpendicular to the lean of each tree. The second core was taken between 90° and 180° from the first. Areas on the stem with defects, burls or potential for rot were avoided. More trees and cores were sampled in old forests to increase chronology length and bolster early chronology replication. Only single cores from 20 AWC trees were collected at Uttertown Bog as this collection was a part of a AWC study ranging from northwestern NJ to southern Maine where sample replication was sacrificed to increase spatial coverage and yet reduce laboratory time (Hopton and Pederson, in press). Despite collecting only a single core from 10 trees per species per site in east Texas, a robust climate response was identified among 12 species (Cook et al., 2001). Though smaller than normal, previous experience suggests that our replication should be adequate.

Tree-ring analysis

Core samples were prepared and analyzed using standard dendrochronological techniques (Stokes and Smiley, 1968; Fritts, 1976; Cook and Kairiukstis, 1990). Cores were visually crossdated by matching the pattern of narrow and wide rings between all samples in each population (Douglass, 1920; Stokes and Smiley, 1968). Annual rings were measured to at least ±0.002 mm. Crossdating was then statistically verified using the program COFECHA (Holmes, 1983). Using these dating methods, annual time series of radial growth were created with dating errors of ±zero years. Cores that correlated poorly in COFECHA were removed from the population prior to chronology development. These cores had low year-to-year variability in growth or unusual growth trends compared to the sampled population.

Raw ring-width measurements were processed into tree-ring chronology form using the ARSTAN method (Cook, 1985; Cook and Kairiukstis, 1990). Before standardization could begin, short periods of distorted radial growth in a few cores were modeled and replaced. Distorted radial growth often occurred after a stem injury or as a branch scar heals. It was visually identified as reaction wood. Ring widths for these periods were filled using dummy variables. A new procedure in ARSTAN recognizes the dummy variables and interpolates low-frequency growth using a 20-year spline. Next, a high-pass filter calculates high-frequency information from the mean chronology. Low-frequency data from the 20-year spline is multiplied by the

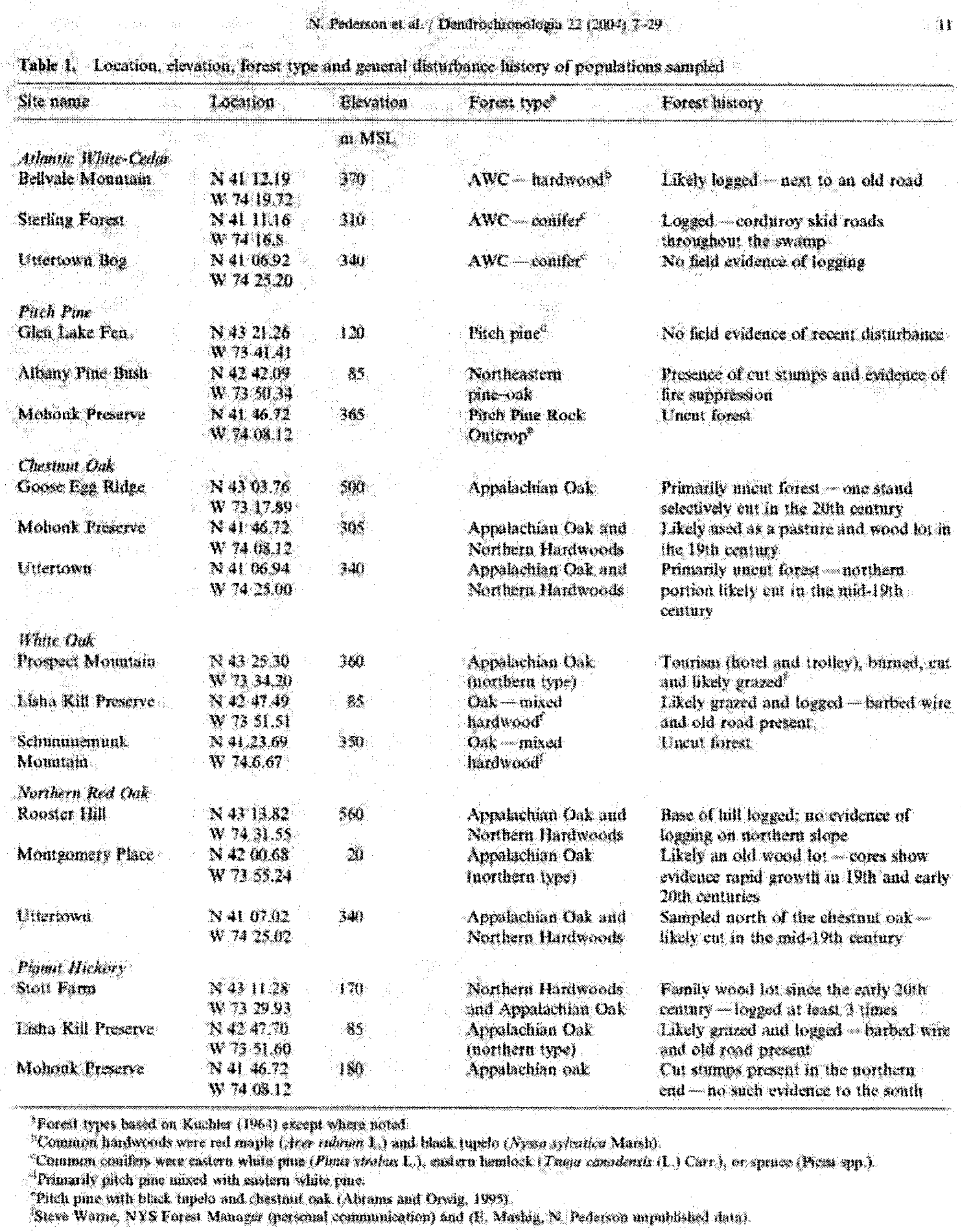

Table 1. Location, elevation, forest type and general disturbance history of populations sampled

Site name	Location	Elevation	Forest type[a]	Forest history
		m MSL		
Atlantic White-Cedar				
Bellvale Mountain	N 41 12.19 W 74 19.72	370	AWC — hardwood[b]	Likely logged — next to an old road
Sterling Forest	N 41 11.16 W 74 16.8	310	AWC — conifer[c]	Logged — corduroy skid roads throughout the swamp
Uttertown Bog	N 41 06.92 W 74 25.20	340	AWC — conifer[c]	No field evidence of logging
Pitch Pine				
Glen Lake Fen	N 43 21.26 W 73 41.41	120	Pitch pine[d]	No field evidence of recent disturbance
Albany Pine Bush	N 42 42.09 W 73 50.34	85	Northeastern pine–oak	Presence of cut stumps and evidence of fire suppression
Mohonk Preserve	N 41 46.72 W 74 08.12	365	Pitch Pine Rock Outcrop[e]	Uncut forest
Chestnut Oak				
Goose Egg Ridge	N 43 03.76 W 73 17.89	500	Appalachian Oak	Primarily uncut forest — one stand selectively cut in the 20th century
Mohonk Preserve	N 41 46.72 W 74 08.12	305	Appalachian Oak and Northern Hardwoods	Likely used as a pasture and wood lot in the 19th century
Uttertown	N 41 06.94 W 74 25.00	340	Appalachian Oak and Northern Hardwoods	Primarily uncut forest — northern portion likely cut in the mid-19th century
White Oak				
Prospect Mountain	N 43 25.30 W 73 34.20	360	Appalachian Oak (northern type)	Tourism (hotel and trolley), burned, cut and likely grazed[f]
Lisha Kill Preserve	N 42 47.49 W 73 51.51	85	Oak — mixed hardwood[f]	Likely grazed and logged — barbed wire and old road present
Schunnemunk Mountain	N 41.23.69 W 74.6.67	350	Oak — mixed hardwood[f]	Uncut forest
Northern Red Oak				
Rooster Hill	N 43 13.82 W 74 31.55	560	Appalachian Oak and Northern Hardwoods	Base of hill logged; no evidence of logging on northern slope
Montgomery Place	N 42 00.68 W 73 55.24	20	Appalachian Oak (northern type)	Likely an old wood lot — cores show evidence rapid growth in 19th and early 20th centuries
Uttertown	N 41 07.02 W 74 25.02	340	Appalachian Oak and Northern Hardwoods	Sampled north of the chestnut oak — likely cut in the mid-19th century
Pignut Hickory				
Stott Farm	N 43 11.28 W 73 29.93	170	Northern Hardwoods and Appalachian Oak	Family wood lot since the early 20th century — logged at least 3 times
Lisha Kill Preserve	N 42 47.70 W 73 51.60	85	Appalachian Oak (northern type)	Likely grazed and logged — barbed wire and old road present
Mohonk Preserve	N 41 46.72 W 74 08.12	180	Appalachian oak	Cut stumps present in the northern end — no such evidence to the south

[a] Forest types based on Kuchler (1964) except where noted.
[b] Common hardwoods were red maple (*Acer rubrum* L.) and black tupelo (*Nyssa sylvatica* Marsh).
[c] Common conifers were eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), or spruce (Picea spp.).
[d] Primarily pitch pine mixed with eastern white pine.
[e] Pitch pine with black tupelo and chestnut oak. (Abrams and Orwig, 1995).
[f] Steve Warne, NYS Forest Manager (personal communication) and (E. Mashig, N. Pederson unpublished data).

high-pass filter data to estimate ring width in place of the distorted growth. This method creates realistic estimates of growth and annual variability for missing or cut data (Fig. 2a). After distorted radial growth was modeled and variance was stabilized using an adaptive power transformation of the raw data (Cook et al., 1992; Cook and Peters, 1997), standardization could proceed.

The goal of standardization was to remove geometric and ecological growth trends while preserving variations that are likely related to climate. Ecological growth trends as defined here result from tree-to-tree competition and stand dynamics that cause short-lived, step-change increases in growth (Lorimer, 1985; Lorimer and Frelich, 1989). Removing ecological growth trends in closed canopied forests is difficult to achieve as disturbance and competition strongly influences growth (Fig. 2b). Our standardization goal was achieved by double detrending each radial growth series. Geometric growth trends were first removed from all series using fitted negative exponential or linear growth curves (Fig. 2c). Second detrending of time series with step-change increases in growth was achieved using flexible cubic smoothing splines (Cook and Peters, 1981) (Figs. 2b) or, occasionally, Hugershoff-form curve (Briffa et al., 2001). The Hugershoff-form curve effectively reduces the influence of short periods of suppressed growth at the beginning of time series while simultaneously preserving long-term trends. Some series had no increase in growth typical of canopy disturbance after the first detrending (Fig. 2d). Growth trends like Fig. 2d are present in several populations region wide. The lack of obvious disturbance in the ring patterns and presence of long-term trends in forests with different histories (Table 1) suggests that these trends may be exogenous and not related to stand dynamics. Therefore, there was no compelling reason to remove these trends. Accordingly, a horizontal line of the arithmetic mean fit was used for the second detrending of these series.

After detrending, individual time series are averaged using a biweight robust mean function to create the mean value function of year-to-year growth for each population (Cook, 1985). Autoregression modeling was used to remove much of the auoregressive properties in the detrended series to create the residual chronology. The residual chronology type contains the least amount of disturbance-related growth, has one of the cleanest expressions of climate, and lacks autocorrelation that can make statistical hypothesis testing difficult (Cook, 1985).

Chronology quality was estimated using rbar (Briffa, 1995) and expressed population signal statistics (Wigley et al., 1984). EPS and rbar are the primary tools in evaluating tree-ring chronology quality (Cook and Kairiukstis, 1990). Rbar is the mean correlation of all growth series within a population. Rbar is independent of sample size and unbiased, though caution is needed when interpreting rbar at very low sample sizes. EPS is a function of rbar and sample size and describes how well a finite sample size estimates the infinite, hypothetical population.

Climate data

The US Historical Climatology Network data set (Easterling et al., 1996) was used to study long-term temperature sensitivity. It is one of the longest, high-quality meteorological data available. While growth does not occur at a monthly time step, only monthly climate data offers a dense network of meteorological data before 1930. The following stations in New York State were used: Albany, Gloversville, Mohonk Preserve, Port Jervis and West Point (Fig. 1b). The common period for the meteorological data was from 1896 to 1994. One year of data was lost due to the 20-month climate window. Therefore, temperature analysis was performed over a 98-year period from 1897 to 1994. All meteorological station data were combined using a mean and variance corrected arithmetic average to create a minimum and maximum monthly time series for the entire HRV.

Temperature response analysis

The temperature response of each population was determined by correlating the residual chronology against a 20-month climate window from prior March to October of the current growth year. Climate during the prior growing season and intervening season can influence a tree's current growth (Fritts, 1976; Kramer and Kozlowski, 1979; Cook and Kairiukstis, 1990). Several physiological factors are responsible for the lag between a prior year's climate and growth. First, pine, oak, and hickory species exhibit determinate growth. Species with determinate growth typically flush once a growing season. Similar to this physiology, some species have preformed shoots in which the number of leaves and amount of growth for the first flush is set during bud formation of the prior year (Kramer and Kozlowski, 1979). For example, shoot elongation in some oaks may occur in less than a month early in the growing season and is a function of the fixed growth in their preformed winter buds (Kozlowski, 1964). Therefore, a good proportion of growth in these species is related to conditions prior to a current year's. Second, non-structural carbon, an important component of bud construction and early leaf development, has a residence time up to 3 5 years in oak (Trumbore et al., 2002). Finally, the season of root growth is longer than shoot growth in some species (Kramer and Kozlowski, 1979). Considering growing season length in the HRV, tree

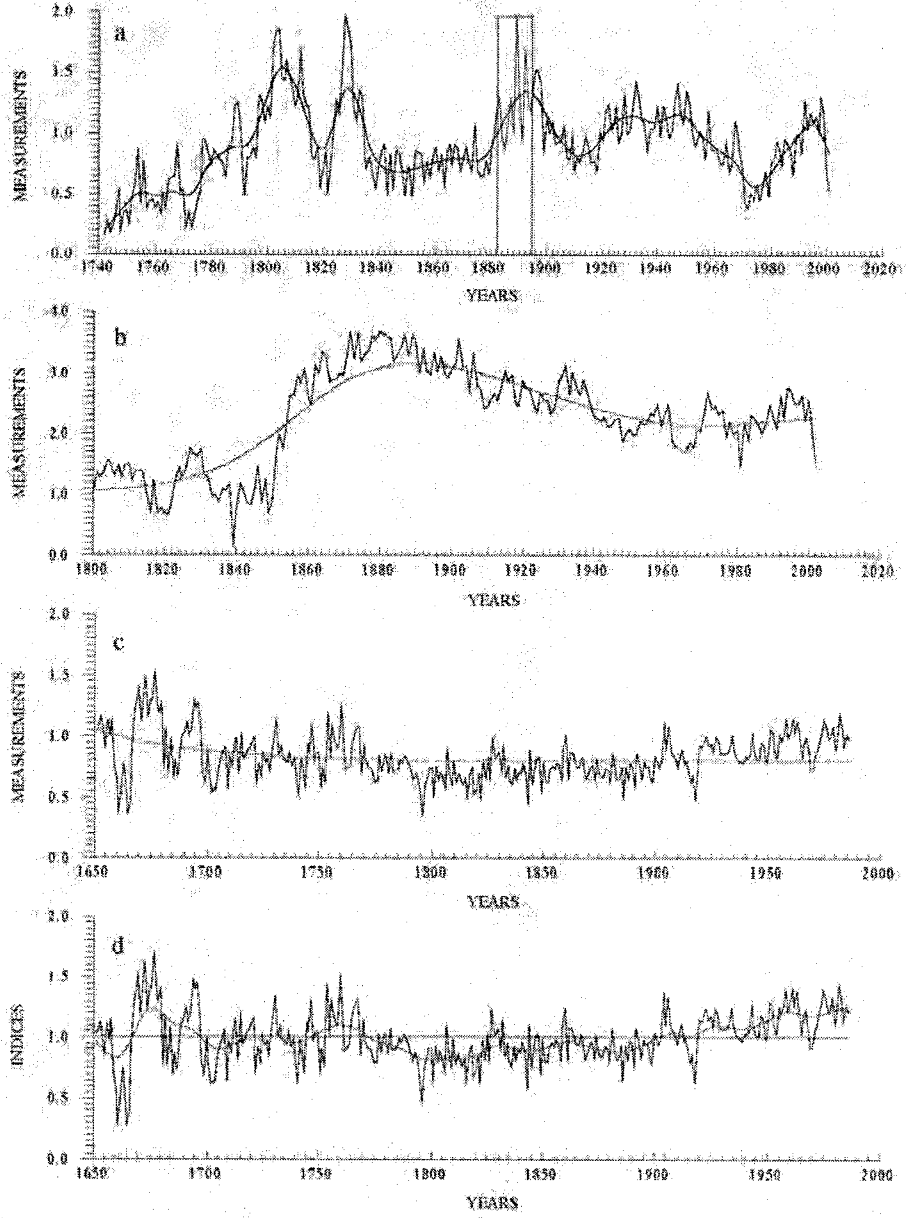

Fig. 2. Examples of: (a) filling of a gap in a series of raw ring width data. The modeled data is the gray line within the boxed area; (b) typical radial growth response to a reduction in competition. The increase in growth following disturbance is detrended using a cubic smoothing spline (Cook and Peters, 1981); (c) detrending of raw ring width data with a fitted negative exponential growth curve; and (d) the resulting indices following detrending of the time series in (c). See text for more details.

phenology, the importance of stored non-structural carbon on growth and its mean residence time, a 20-month climatic window is biologically meaningful. The residual chronology was correlated against prewhitened climate data since time series of temperature data can also have significant autocorrelation.

Each chronology was correlated against the nearest meteorological station. Because there are no long, local meteorological stations in the northern HRV, Gloversville was used in this subregion. Gloversville's relatively high elevation vs. Albany (247 m vs. 84 m MSL, respectively) and location in the Adirondack Mountains foothills better matches the settings of most northern HRV populations. Albany was used for analysis of the north-central HRV populations. The Mohonk Preserve meteorological station was used for analysis of mid-HRV populations. Most sites in the southern end of the transect are on the western side of the Hudson Highlands. Preliminary analysis indicated that Port Jervis station data produced more consistent results vs. most southern populations than the West Point station. The Schunnemunk Mountain white oak population, on the eastern side of the Hudson Highlands, was correlated to West Point data.

A one-tailed test was used for correlation analysis since only positive relations between temperature and growth are considered. Temperature was considered a significant factor of growth at the $p \leqslant 0.05$ level. During preliminary analysis, it was observed that winter months were an important factor of growth. Correlation analysis was then performed on a common winter season for each species.

Principal component analysis

A rotated PCA was performed on the residual chronologies to objectively identify common modes of variation through time among species to create a time series of principal component scores. Varimax rotation is the orthogonal rotation of axes of a subset of unrotated principal components. The normalized varimax method of rotating eigenvectors preserves orthogonality of the factor loadings and increases interpretability (Richman, 1986). It eases interpretation because original variables often load onto one or, at most, a few factors and each factor typically is represented by a small number of variables. We use the term "rotated factors" to distinguish the varimax rotation of eigenvectors from the unrotated principal components. The number of eigenvectors retained was determined by the Monte Carlo "Rule-*N*" method (Preisendorfer et al., 1981). The period of analysis was 1897 1994. PCA enabled us to investigate the temperature sensitivity of the southern temperate ecosystem at regional and subregional scales. Preliminary PCA runs indicated a specific oak hickory grouping. Consequently, a separate PCA was performed on the oak and hickory populations at both the geographic scales.

The subregions analyzed were the: (1) northern HRV composed of Prospect Mountain white oak, Rooster Hill red oak, Glen Lake Fen pitch pine, Goose Egg Ridge chestnut oak and Stott Farm pignut hickory; (2) north-central HRV composed of Lisha Kill Preserve white oak and pignut hickory and the Albany Pine Bush pitch pine; (3) mid-HRV composed of Montgomery Place red oak and Mohonk Preserve chestnut oak, pignut hickory and pitch pine; and (4) southern HRV composed of Schunnemunk Mountain white oak, Sterling Forest AWC, and Uttertown chestnut and red oak. Only the Sterling Forest AWC population was used for the southern HRV subregion so the southern HRV PCA was not biased towards AWC. Sterling Forest was chosen a priori because of its central location among the AWC populations.

The retained principal component scores for the HRV were correlated against the averaged five station temperature series. Each subregion's scores were correlated against the local meteorological station: Gloversville vs. northern HRV; Albany vs. north-central HRV; Mohonk Preserve vs. mid-HRV; Port Jervis vs. southern HRV. Correlation analysis was performed in the same manner as with the tree-ring records.

Results

Tree-ring chronology characteristics

All chronologies met the minimum age requirement of the study and had an average EPS > 0.85 despite frequent forest disturbance and conservative detrending methods (Table 2). Chestnut oak had the highest average EPS across populations while pignut hickory had the lowest. Rbar values indicated a fairly strong overall chronology signal for each population. Pitch pine had the highest average rbar across populations while pignut hickory had the lowest. Chronology statistics indicate a strong common signal in uneven-aged populations.

Principal component analysis

PCA indicated a significant amount of common growth variation across all populations in the HRV (Table 3). Only two rotated factors were retained. Rotated factor one (RF1) accounted for 27.3% of the common growth variation while rotated factor two (RF2) accounted for 19.9%. Loadings onto RF1 were dominated by oak, primarily by chestnut and white oak, while loadings onto RF2 were dominated by AWC.

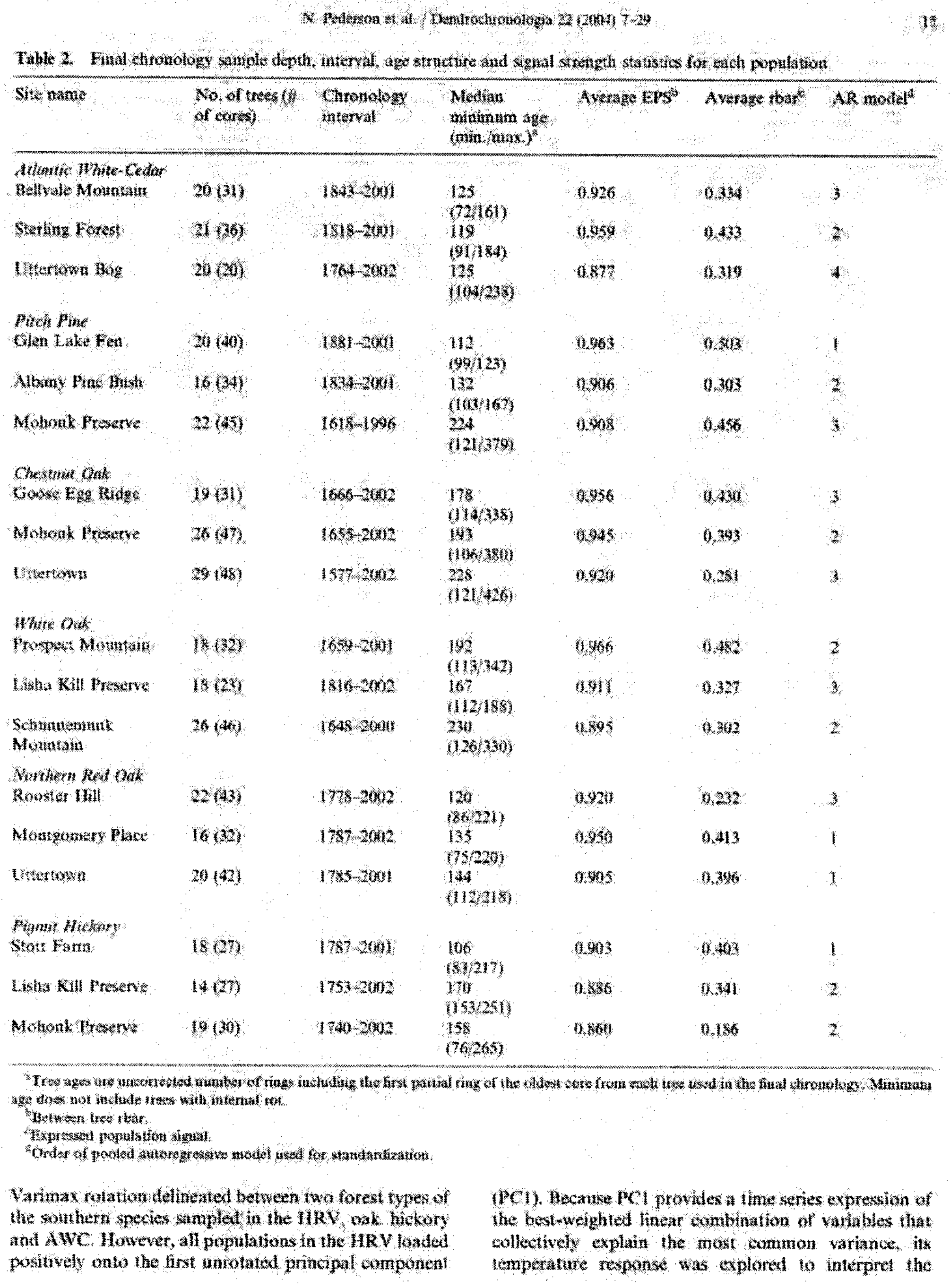

Table 2. Final chronology sample depth, interval, age structure and signal strength statistics for each population

Site name	No. of trees (# of cores)	Chronology interval	Median minimum age (min./max.)[a]	Average EPS[b]	Average rbar[c]	AR model[d]
Atlantic White-Cedar						
Bellvale Mountain	20 (31)	1843–2001	125 (72/161)	0.926	0.334	3
Sterling Forest	21 (36)	1818–2001	119 (91/184)	0.959	0.433	2
Uttertown Bog	20 (20)	1764–2002	125 (104/238)	0.877	0.319	4
Pitch Pine						
Glen Lake Fen	20 (40)	1881–2001	112 (99/123)	0.963	0.503	1
Albany Pine Bush	16 (34)	1834–2001	132 (103/167)	0.906	0.303	2
Mohonk Preserve	22 (45)	1618–1996	224 (121/379)	0.908	0.456	3
Chestnut Oak						
Goose Egg Ridge	19 (31)	1666–2002	178 (114/338)	0.956	0.430	3
Mohonk Preserve	26 (47)	1655–2002	193 (106/380)	0.945	0.393	2
Uttertown	29 (48)	1577–2002	228 (121/426)	0.920	0.281	3
White Oak						
Prospect Mountain	18 (32)	1659–2001	192 (113/342)	0.966	0.482	2
Lisha Kill Preserve	18 (23)	1816–2002	167 (112/188)	0.911	0.327	3
Schunnemunk Mountain	26 (46)	1648–2000	230 (126/330)	0.895	0.302	2
Northern Red Oak						
Rooster Hill	22 (43)	1778–2002	120 (86/221)	0.920	0.232	3
Montgomery Place	16 (32)	1787–2002	135 (75/220)	0.950	0.413	1
Uttertown	20 (42)	1785–2001	144 (112/218)	0.905	0.396	1
Pignut Hickory						
Stott Farm	18 (27)	1787–2001	106 (83/217)	0.903	0.403	1
Lisha Kill Preserve	14 (27)	1753–2002	170 (153/251)	0.886	0.341	2
Mohonk Preserve	19 (30)	1740–2002	158 (76/265)	0.860	0.186	2

[a] Tree ages are uncorrected number of rings including the first partial ring of the oldest core from each tree used in the final chronology. Minimum age does not include trees with internal rot.

[b] Between tree rbar.

[c] Expressed population signal.

[d] Order of pooled autoregressive model used for standardization.

Varimax rotation delineated between two forest types of the southern species sampled in the HRV, oak hickory and AWC. However, all populations in the HRV loaded positively onto the first unrotated principal component (PC1). Because PC1 provides a time series expression of the best-weighted linear combination of variables that collectively explain the most common variance, its temperature response was explored to interpret the

Table 3. Principal component analysis loading factors and percent common variance for all residual and only oak and hickory chronologies

Populations	Factor loading			
	All populations			Oak–hickory
	Unrotated eigen. 1	Rotated factor 1	Rotated factor 2	Unrotated eigen. 1
Bellvale Mountain. AWC	0.224	0.064	0.874	—
Sterling Forest AWC	0.230	0.174	0.881	—
Uttertown AWC	0.260	0.075	0.887	—
Glen Lake Fen pitch pine	0.142	0.215	0.319	—
Albany Pine Bush pitch pine	0.111	0.094	0.351	—
Mohonk Preserve pitch pine	0.174	0.312	0.323	—
Goose Egg Ridge chestnut oak	0.282	0.812	0.109	0.335
Mohonk Preserve chestnut oak	0.322	0.747	0.369	0.360
Uttertown chestnut oak	0.274	0.542	0.440	0.301
Prospect Mountain. white oak	0.274	0.703	0.225	0.314
Lisha Kill Preserve white oak	0.262	0.725	0.145	0.307
Schunnemunk Mtn. white oak	0.209	0.568	0.125	0.253
Rooster Hill northern red oak	0.205	0.647	0.002	0.250
Montgomery Place northern red oak	0.234	0.518	0.301	0.260
Uttertown northern red oak	0.272	0.484	0.512	0.292
Stott Farm pignut hickory	0.232	0.588	0.199	0.250
Lisha Kill Preserve pignut hickory	0.203	0.581	0.081	0.260
Mohonk Preserve pignut hickory	0.234	0.513	0.308	0.292
Common variance (%)	36.0	27.3	19.9	44.9

Table 4. Principal component analysis loading factors for eigenvector 1 and percent common variance for all residual and only oak–hickory chronologies

Subregion	All populations		Oak–hickory	
	Factor loading	Variance (%)	Factor loading	Variance (%)
Northern Hudson Valley		52.8		62.8
Goose Egg Ridge chestnut oak	0.549		0.565	
Prospect Mountain white oak	0.494		0.516	
Rooster Hill northern red oak	0.442		0.459	
Stott Farm pignut hickory	0.431		0.451	
Glen Lake Fen pitch pine	0.270		—	
North-central Hudson Valley		54.2		75.8
Lisha Kill Preserve pignut hickory	0.656		0.707	
Lisha Kill Preserve white oak	0.647		0.707	
Albany Pine Bush pitch pine	0.387		—	
Mid-Hudson valley		55.9		66.9
Mohonk Preserve pignut hickory	0.552		0.593	
Mohonk Preserve chestnut oak	0.548		0.591	
Montgomery Place northern red oak	0.488		0.547	
Mohonk Preserve pitch pine	0.396		—	
Southern Hudson valley		59.2		70.3
Uttertown northern red oak	0.580		0.617	
Uttertown chestnut oak	0.575		0.622	
Schunnemunk Mountain white oak	0.417		0.482	
Sterling Forest Atlantic white-cedar	0.399		—	
Mean	—	55.5	—	69.0

influence of temperature for the southern temperate ecosystem. PC1 accounted for 36% of the common growth variation among all populations. PCA analysis of oak hickory populations revealed only one significant principal component, which accounted for 44.9% of the common growth variation. Chestnut and white oak had the highest loadings on this unrotated principal component (PC OH).

Within each subregion only PC1 was significant. Mean common growth variation among subregional populations was 55.5% (SD = 2.8%) (Table 4). Oak and hickory species loaded nearly equally onto the first principal component in each subregion while conifers consistently loaded the lowest. PCA of oak and hickory populations in each subregion revealed a higher amount of common growth variation (mean = 69.0%, SD = 5.5%). Loading order did not change significantly from the PCA of all species in each subregion. The north-central results must be cautiously interpreted as only two populations were available for analysis.

Species response to temperature

AWC growth is significantly correlated to winter and growing season temperature (Figs. 3a c). Winter temperatures (November March) had the strongest correlation to growth and were significantly correlated at the $p < 0.001$ level (Table 5). The most consistent correlations during the growing season were minimum temperatures in July and August.

Northern and north-central HRV pitch pine populations were significantly correlated to winter (November - March) temperatures (Figs. 3d and e; Table 5). Prior November and current February temperatures were significant factors of growth in the northern HRV population. North-central HRV growth was significantly correlated to minimum March and April temperatures. The mid-HRV pitch pine population was significantly correlated to prior minimum May and July temperature prior maximum July and August, but not winter (Fig. 3f).

Chestnut oak growth was significantly correlated to winter (December January) temperatures in the mid- and southern HRV (Table 5). Northern HRV growth was significantly correlated to prior maximum April, May and June and prior minimum October temperatures (Fig. 4a). Mid-HRV growth was significantly correlated to prior July, current January and current minimum September temperatures (Fig. 4b). Southern HRV growth was significantly correlated to prior April temperatures prior maximum December and current January temperatures (Fig. 4c).

White oak growth was significantly correlated to January temperatures in the north-central and southern HRV (Figs. 4d f; Table 5). The northern HRV population showed very low sensitivity to temperature (Fig. 4d). The north-central population was only significantly correlated to maximum January temperatures. Southern HRV growth was significantly correlated to current January and October maximum temperatures.

Northern red oak did not have a strong relation to January temperatures (Figs. 5a c; Table 5). Northern HRV growth was significantly correlated to prior maximum March, minimum October, current maximum January, September and October temperatures.

Pignut hickory was best correlated to winter temperatures only in the mid-HRV (Figs. 5d f; Table 5). Northern HRV growth was significantly correlated to prior maximum May and June and current minimum July temperatures. North-central HRV growth was significantly correlated to prior and current maximum September and prior November temperatures. Mid-HRV growth was only correlated to current September temperatures.

Ecosystem temperature response

Ecosystem temperature response for the HRV is shown in Fig. 6. RF1 was only significantly correlated to prior minimum October temperatures. RF2 was most strongly correlated to winter (December February) and April temperatures. RF2 was also significantly correlated to 2 months during the growing season, minimum July and maximum October temperatures. PC1 was significantly correlated to January temperatures. PC OH was significantly correlated to prior minimum October and current January temperatures.

Subregional ecosystem temperature response revealed a geographic pattern of increasing winter temperature sensitivity moving south (Fig. 7a d). Northern HRV growth was significantly correlated to prior April and June maximum and current July minimum temperatures. North-central HRV growth was significantly correlated to prior maximum November and current maximum September temperatures. Mid-HRV growth was significantly correlated to prior maximum July and current minimum September temperatures. Southern HRV growth was significantly correlated to prior maximum December, current January and current maximum October temperatures. Temperature response of oak hickory PCA scores only slightly altered the pattern (Fig. 7e h). Perhaps the most important change was a significant correlation of growth to January temperatures in the mid-HRV.

Discussion

Monthly and seasonal winter temperatures are more limiting than growing season temperatures to annual radial growth of NRM species in the HRV (Figs. 3 4 and 6 7; Table 5). At the southern temperate ecosystem level January temperatures had the strongest influence

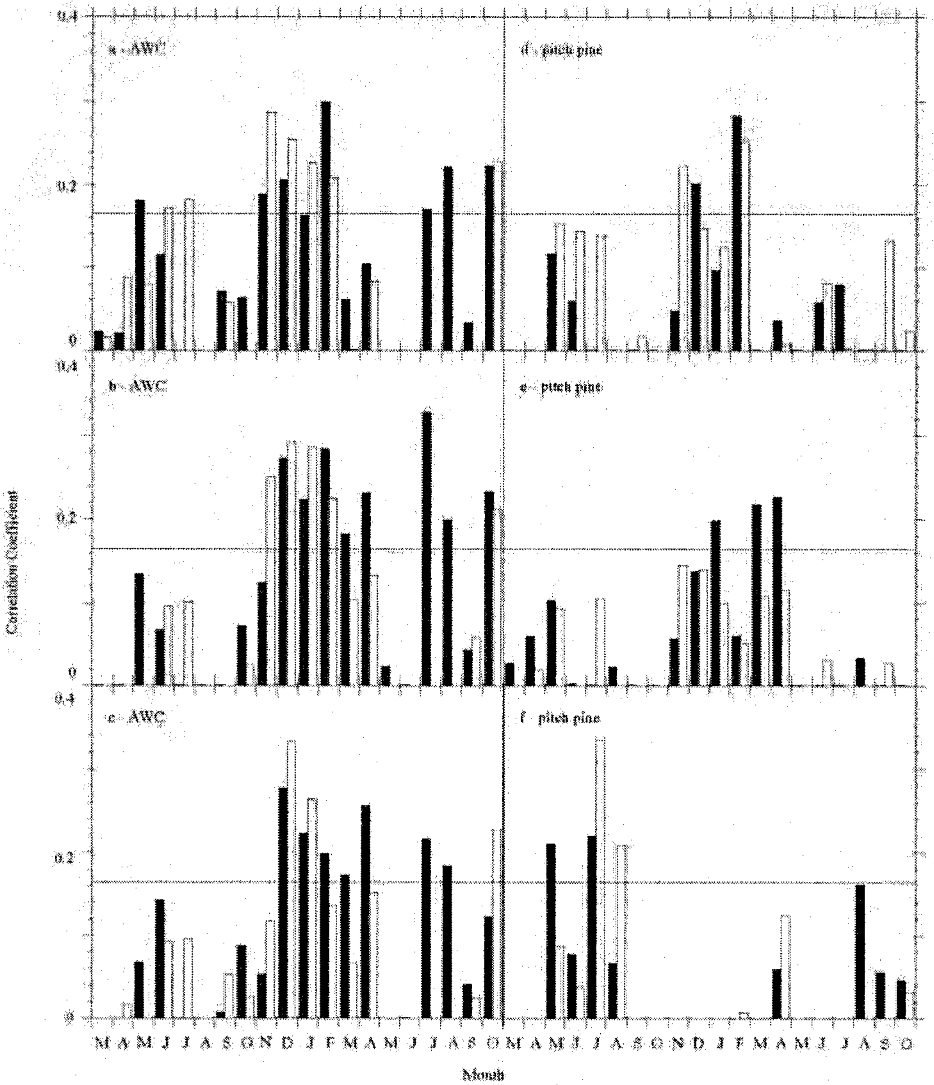

Fig. 3. Correlation between average monthly minimum temperatures (solid bars) and average monthly maximum temperatures (open bars) and residual chronologies of AWC arranged north–south: (a) Bellvale Mountain, NY; (b) Sterling Forest, NY; and (c) Uttertown Bog, NJ and pitch pine arranged north–south: (d) Glen Lake Fen, NY; (e) Albany Pine Bush, NY; and (f) Mohonk Preserve, NY. Thin, horizontal line indicates a significant correlation at the 95% confidence limit for a one-tailed test.

on growth (Fig. 6a). Although an unrotated eigenvector may minimize the complexity of a multivariate system (Dommengel and Latif, 2002), it does isolate the common variance among all populations. Much of the common variance in PC1 is related to growing season drought (N. Pederson, unpublished data) which helps

Table 5. Relations between winter temperatures and radial growth

Site name	Residual chronology correlation (p value)	
	T_{min}	T_{max}
Atlantic White-Cedar[a]		
Bellvale Mountain	0.337***	0.317***
Sterling Forest	0.380***	0.409***
Uttertown Bog	0.360***	0.331***
Pitch Pine[a]		
Glen Lake Fen	0.249**	0.213*
Albany Pine Bush	0.252**	0.200*
Mohonk Preserve	−0.076	−0.131
Chestnut Oak[b]		
Goose Egg Ridge	0.072	0.126
Mohonk Preserve	0.187*	0.207*
Uttertown	0.192*	0.198*
White Oak[c]		
Prospect Mountain	0.015	0.070
Lisha Kill Preserve	0.154	0.211*
Schunnemunk Mountain	0.168**	0.214**
Northern Red Oak[c]		
Rooster Hill	0.119	0.179*
Montgomery Place	0.105	0.105
Uttertown	0.113	0.140
Pignut Hickory[d]		
Stott Farm	−0.042	−0.091
Lisha Kill Preserve	0.030	0.002
Mohonk Preserve	0.159	0.126

T_{min} = average minimum monthly temperatures; T_{max} = average minimum monthly temperatures; ***represents $p \leq 0.001$; **represents $p \leq 0.010$; *represents $p \leq 0.050$.

[a] Season = November–March.

[b] Season = December–January.

[c] Season = January.

[d] Season = January–February.

explain the rather equitable loadings on PC1 (Table 3). However, growth of populations with the highest loadings on PC1 also tends to be more strongly correlated to winter temperatures or are located in the southern half of the HRV. Therefore, species and geography seem to be most responsible for the large-scale, southern temperate ecosystem response to winter temperatures. The high sensitivity of conifers at the northern and southern end of the HRV (Fig. 3) strengthened southern temperate ecosystem response. The January response of the oak hickory ecosystem across the HRV (Fig. 6d) is weaker than the southern temperate ecosystem response (Fig. 6a). Winter temperatures have been found to constrain radial growth in different temperate species and ecosystems (Brubaker, 1980; Conkey, 1982; Cook et al., 1987, 2001; D'Arrigo et al., 1997, 2001; Pan et al., 1997; Rubino and McCarthy, 2000; Tardif et al., 2001). Only Brubaker (1980) demonstrated the importance of winter temperatures for multiple species. Winter temperatures are hypothesized to be one of the dominant controls on ecotone position (Neilson, 1993). The HRV is a northward extension of southern deciduous forest types (Bray, 1915; Braun, 1950; Bailey, 1995) and its position correlates to the average location of the convergence of winter Arctic and Pacific Frontal Zones (Bryson et al., 1970). Our results support the hypothesis that ecotone position may be related to winter temperature sensitivity.

Curiously, there is a geographic pattern of winter temperature response at the subregional scale (Fig. 7). January temperatures most strongly limit radial growth in the lower half of the HRV. Although January temperatures limit oak and hickory growth (PC OH) across the entire HRV (Fig. 6d), the geographic pattern is driven primarily by the temperature response of chestnut and white oak which often loaded the highest

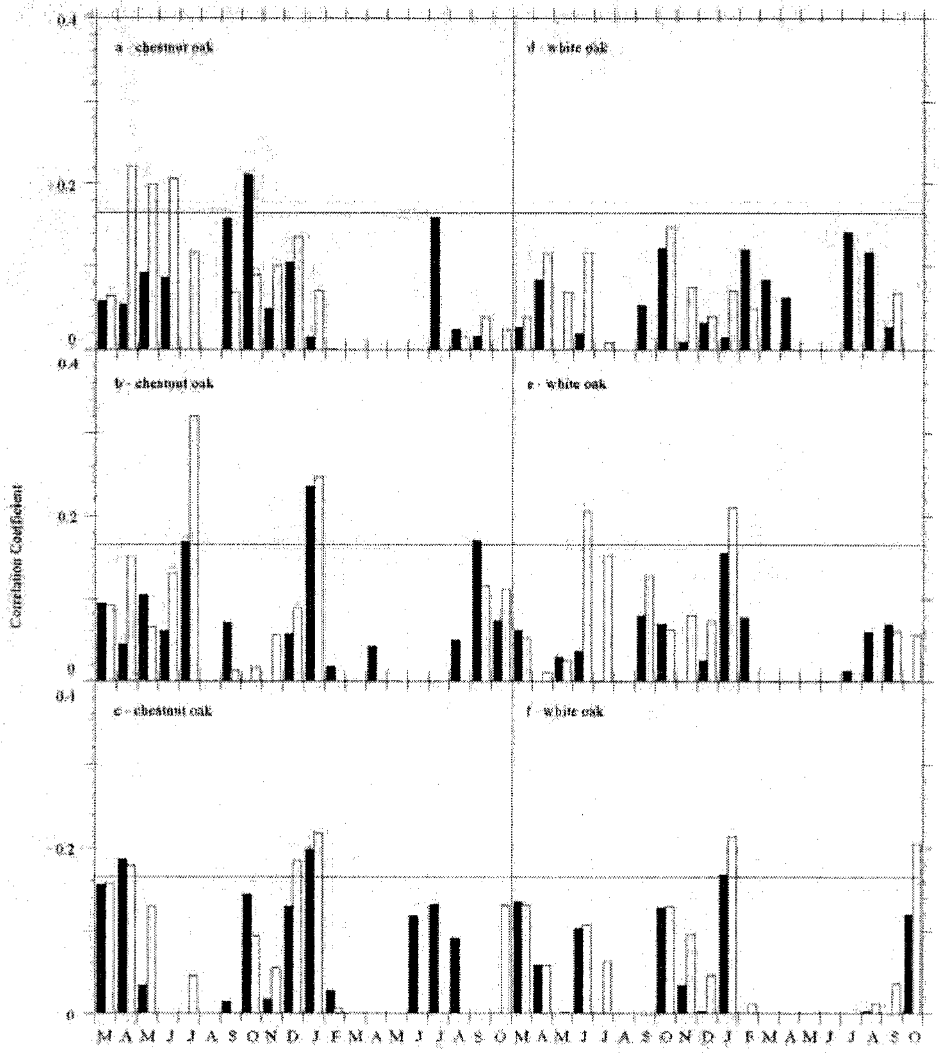

Fig. 4. Same as Fig. 3 except for chestnut oak arranged north–south: (a) Goose Egg State Forest, NY; (b) Mohonk Preserve, NY; and (c) Uttertown, NJ and white oak arranged north–south: (d) Prospect Mountain, NY; (e) Lisha Kill Preserve, NY; and (f) Schunnemunk Mountain, NY. Thin, horizontal line indicates a significant correlation at the 95% confidence limit for a one-tailed test.

first principal component in each subregion. The January response in the southern half of the HRV (Figs. 7(g and h)) strongly resembles the patterns of chestnut and white oak (Fig. 4; Table 5). Northern red oak and pignut hickory contribute to the geographic pattern, though to a lesser degree (Figs. 5c and f; Tables 3–5). The cause of the geographic pattern is not certain.

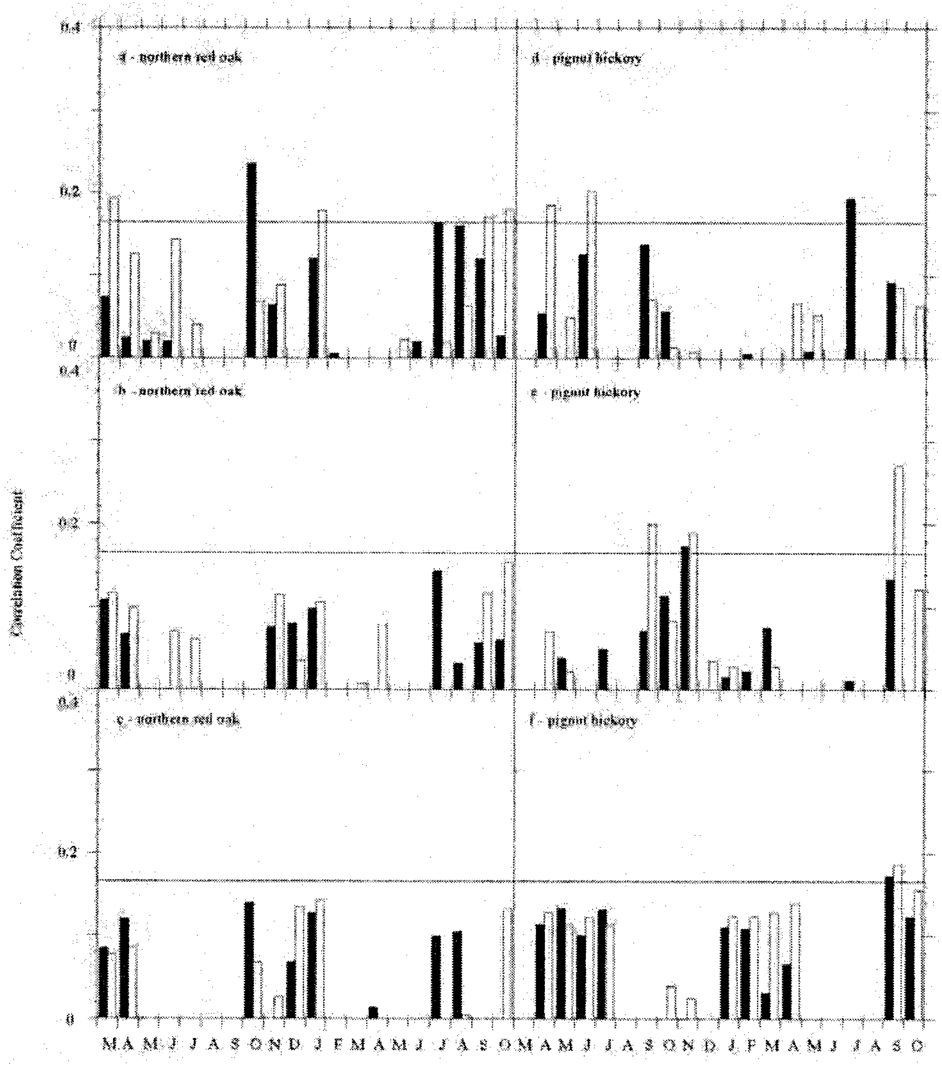

Fig. 5. Same as Fig. 3 except for northern red oak arranged north–south: (a) Rooster Hill, NY; (b) Montgomery Place, NY; and (c) Uttertown, NJ and pignut hickory arranged north–south: (d) Argyle, NY; (e) Lisha Kill, NY; and (f) Mohonk Preserve, NY. Thin, horizontal line indicates a significant correlation at the 95% confidence limit for a one-tailed test.

Hypothetically, the geographic temperature response could result from the potential negative influence of winter xylem embolisms on growth (Zimmermann, 1983; Cochard and Tyree, 1990; Sperry and Sullivan, 1992; Sperry et al., 1994; Field and Brodribb, 2001). Winter embolisms disrupt the conductance of water within a tree's stem. Oaks often have high levels of xylem embolism by winter's end, even in warm

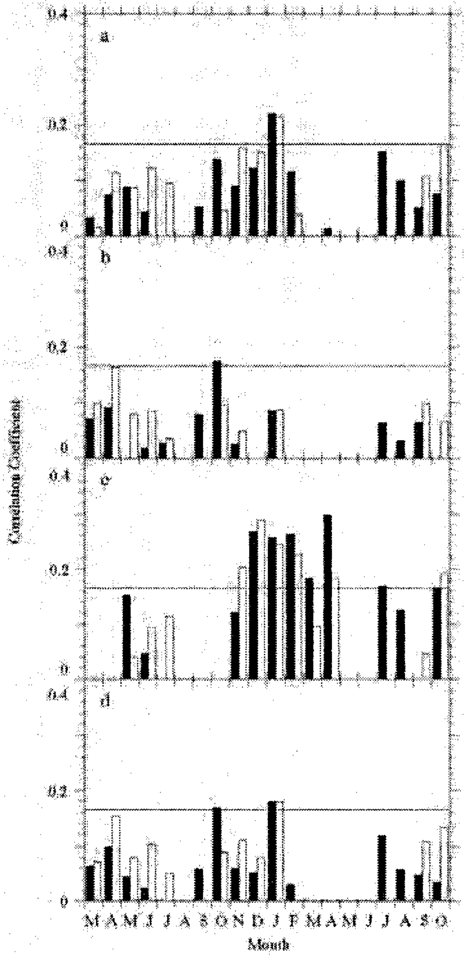

Fig. 6. Correlation between average monthly minimum temperatures (solid bars) and average monthly maximum temperatures (open bars) against HRV PCA scores of (a) unrotated eigenvector 1; (b) rotated eigenvector factor 1; (c) rotated eigenvector factor 2; and (d) eigenvector 1 scores for only oak and hickory species. Thin, horizontal line indicates a significant correlation at the 95% confidence limit for a one-tailed test.

temperate and Mediterranean climates (Cochard and Tyree, 1990; Sperry and Sullivan, 1992; Sperry et al., 1994; Tyree and Cochard, 1996; Tognetti et al., 1998; Cavender-Bares and Holbrook, 2001). Recovery of water conductance in oaks is made through the production of earlywood (or pore vessels) before leaf-out (Sperry et al., 1994). Energy that could be used for growth would likely be used for winter embolism recovery. Because winter embolism is a physiological limitation of oak and hickory trees, it ought to be a constant factor across the HRV. Consequently, there must be other factors for the observed geographic variation in January temperature sensitivity.

An interaction between snow cover and fine root mortality are additional factors that could account for the stronger winter temperature response in the southern HRV. A deep snow pack in late winter has been shown to effectively reduce radial growth rates by maintaining low soil temperatures and delaying initiation of cambial expansion (Graumlich and Brubaker, 1986; Gedalof and Smith, 2001; Peterson and Peterson, 2001; Peterson et al., 2002). At treeline a lack of snow cover can also have a detrimental effect through increased winter desiccation and erosion of cambium and foliage from wind-blown snow and ice crystals (e.g. Payette et al., 1996; Kajimoto et al., 2002). We hypothesize that reduced snow cover in the southern half of the HRV reduces growth through the increase of fine root mortality.

From December March average snow cover ranges from 5% to 25% in the southern HRV to >75% in the Adirondack Mountains (Groisman et al., 1994; Groisman and Davies, 2001). Effective freeze-thaw days, which are freeze-thaw days with less than 7.5 cm of snow, occur twice as often in the lower HRV than the Adirondack Mountains (Schmidlin et al., 1987). Snow cover 7.5 cm deep can reduce the daily temperature range by roughly 50% (Geiger, 1957). Differences in snow cover from north to south in the HRV may create a significant gradient in winter soil temperature.

Roots are the least cold hardy part of a plant. When snow cover was removed in a natural forest setting, fine root mortality doubled even though mild winter conditions only occasionally drove upper soil temperatures down to −4 °C (Hardy et al., 2001; Tierney et al., 2001). Root damage combined with stem embolism is more highly correlated to reduced xylem conductance and increased shoot dieback than stem damage alone in yellow (*B. alleghaniensis* Britton) and paper birch (Cox and Malcolm, 1997; Cox and Zhu, 2003). Therefore, the potential impact of annual snow cover on a tree's roots may be the most logical explanation of the geographic relation between winter temperatures and radial growth in the HRV. Further investigation requires comparison of snow depths with temperature data in assessment of radial growth.

Winter temperatures are the strongest temperature factor of NRM growth in the HRV. Increased winter temperatures in areas of inconsistent snow pack may mean less winter damage to roots, which may mean less of a growth limitation. Although future climate

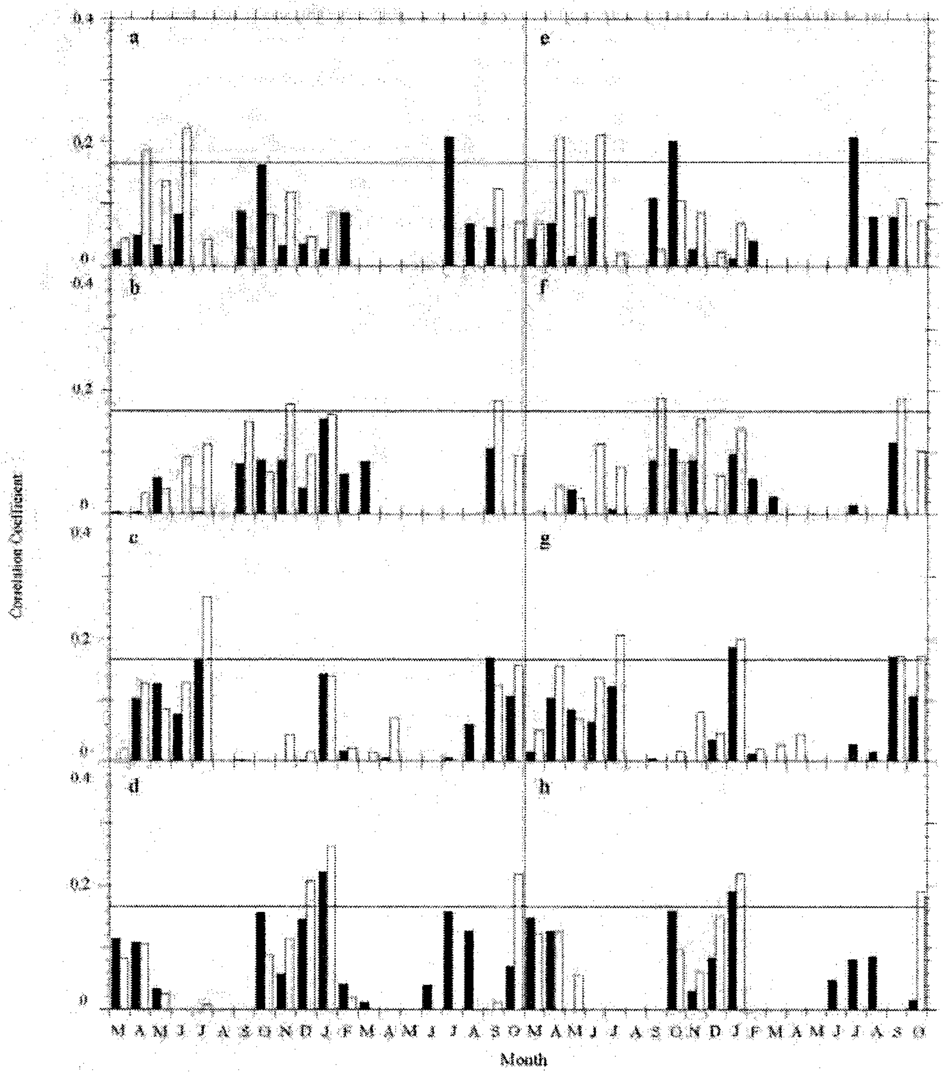

Fig. 7. Same as Fig. 6 except for PCA unrotated eigenvector 1 scores at (a) northern Hudson Valley; (b) north-central Hudson Valley; (c) mid-Hudson Valley; and (d) southern Hudson Valley. (e–h) For the same subregions, but do not include conifer populations. Thin, horizontal line indicates a significant correlation at the 95% confidence limit for a one-tailed test.

warming may reduce productivity and carbon uptake in regions that currently have a consistent annual snow pack (Groffman et al., 2001), it could be that warmer winters in regions without a regular snow pack like the lower HRV may experience increased tree growth and carbon uptake.

The most consistent response of the oak hickory ecosystem is the significant correlation to prior October minimum temperatures (Figs. 6b and d). Although rotated and unrotated eigenvector analysis can detect local and global problems differently (Dommenget and Latif, 2002), both RF1 and PC OH find prior October temperatures to be important for oak hickory growth. Several physiological processes occur early in the fall season (Kramer and Kozlowski, 1979). For example, between 1883 and 1912 in northern Ohio, at roughly the same latitude as the lower HRV, leaf color change was completed in pignut hickory and white oak around October 6 and October 17, respectively (Fig. 4 in Lechowicz, 1984). Deciduous trees translocate nutrients from leaves into branches and buds before leaf senescence (Chabot and Hicks, 1982). Warmer temperatures may allow an extended period of nutrient recovery or rapid rates of recovery prior to leaf fall. Considering that many oak and hickory have determinate shoot growth, completion of these physiological processes is likely important the following year.

Differences in winter temperature response are apparent between species. AWC and pitch pine are more sensitive to winter temperatures and a longer winter season than oak or hickory (Figs. 3–5; Table 5). Pines are also more sensitive to temperature than hardwoods in the upper Great Lakes (Graumlich, 1993). Differences in winter temperature sensitivity between conifers and broad-leaved trees could result from a couple of mechanisms. Temperate conifers can have a positive carbon gain on warm winter days when their leaves are not frozen (Chabot and Hicks, 1982; Havranek and Tranquillini, 1995). In fact, non-structural carbon in xylem, needles and bark varies in amount and quality due to metabolic activity on warm winter days (Havranek and Tranquillini, 1995). However, maintenance of foliage throughout winter makes conifers more susceptible to damage from freezing, snow and ice accumulation or winter desiccation. Differing winter temperature sensitivities of conifers and broad-leaved species are likely a result of contrasting physiological traits.

Winter sensitivity of AWC and pitch pine in the HRV is similar to loblolly pine at its northern range limit (Cook et al., 2001). Research at southern latitudes is needed to determine if the winter temperature sensitivity exists only at NRM for AWC and pitch pine like loblolly pine.

Oak and hickory are not strongly limited by winter temperatures at NRM locations like AWC and pitch pine (Figs. 4, 5 and 7e). Our results suggest that conifers and oak and hickory may have significantly different temperature sensitivities at NRMs and perhaps, contrasting patterns of winter temperature response across latitudes.

Temperature sensitivity in oaks may be determined at the subgenus level. Chestnut and white oak is more sensitive to January temperatures in the southern half of the HRV than northern red oak. Our results support physiologically based research that found white oaks to be more susceptible to freezing than red oaks in northern Florida (Cavender-Bares and Holbrook, 2001). White and red oak subgenus groups also have distinct climatic response across a drought gradient in east Texas (Cook et al., 2001). More research is needed to verify whether the differences in temperature response between red and white oaks are consistent for a larger number of species.

AWC growth is most sensitive to temperature followed somewhat closely by pitch pine and distantly by chestnut oak, pignut hickory, white and northern red oak (Figs. 3–5). Only AWC is correlated to summer temperatures. AWC's strong temperature response accounts for the second rotated eigenvector factor of the HRV (Tables 3 and 5). The high sensitivity of AWC agrees with a study of seven separate AWC populations from New Jersey to Maine where temperature was the most important climatic factor of growth along its northern range limit (Hopton, Pederson, in press). Of species studied in temperate eastern North America, AWC's sensitivity to temperature is exceptional. Red spruce is as temperature-sensitive as AWC in the northeastern US, especially at high elevations (Conkey, 1986; Cook et al., 1987). However, red spruce's growing season sensitivity was related to wood density, not ring width (Conkey, 1982, 1986). Of the species studied in temperate eastern North America, AWC appears to have the best potential for reconstruction of historical temperature variations.

Chestnut oak is the most sensitive oak (Figs. 4 and 5; Table 5). Its higher sensitivity to spring temperatures may help explain its more southerly distribution and lack of occurrence in the Adirondack Mountains of New York State. A late spring and a shorter growing season may put chestnut oak at a competitive disadvantage in northerly locations.

Pignut hickory's late growing season temperature response is the most different of the species studied (Figs. 5e and f). Its climate response has rarely been studied (Hill, 1982; Lin and Muller, 1993; Orwig and Abrams, 1997; Abrams et al., 1998). Why pignut hickory is most sensitive to late growing season temperatures is not clear. It seems like the late-season temperature response would be related to physiological activities and determinate shoot growth as discussed above.

Most differences in temperature response between species were found at the margins of the growing season and may be related to phenology. Phenology of the temperate forest is thought to be temperature driven (Kramer et al., 2000). It is also thought to be an important contributor to species distribution (Chuine and Beaubien, 2001) and growth response to climate change (Kramer et al., 2000). However, much more work is needed to determine if differences in radial-growth temperature sensitivity in the HRV contribute to species distribution.

Local site conditions may play an important role in temperature sensitivity. For example, the absence of a winter response in the mid-HRV pitch pine is conspicuous and runs counter to most of our findings (Fig. 3f). This population grows on an outcrop of conglomerate bedrock while the other pitch pine populations grow in deeper soil. Sandy soils, with a higher amount of pore space, are more conducive to cold air seepage (Kramer and Kozlowski, 1979). It is possible that bedrock acts as an insulator of tree roots.

Conclusion

Winter temperatures are the strongest and most consistent temperature factors of radial growth of NRM species in the HRV. Differences between species suggest that temperature sensitivity may be related to phenology and life history traits. AWC and pitch pine are sensitive to the entire winter season while oak and hickory are primarily sensitive to January temperatures. These differences may have important ecological implications. For example, a shortening of the winter season would favor AWC and pitch pine more than oak and hickory. It is not clear that our results are applicable to the same species in other regions or species from different biomes in our study region. If these results are indicative of the subtle influence of temperature on growth, they suggest that more broad-scale research is needed at the species level.

PCA indicated a strong common signal of radial growth at local and regional scales across multiple species in the HRV. Previous multi-site network studies using multiple species show a strong climate signal across a drought and temperature gradient in eastern North America (Graumlich, 1993; Cook et al., 2001). Our results confirm these prior studies. They also indicate that climate has a strong influence on tree growth in forests with different land-use histories ranging from those in an old-growth condition to those repeatedly cut.

The varying influence of temperature at the species and ecosystem level at different geographic scales has important implications in forecasting the impact of climate change on forested ecosystems. As has been shown for eastern hemlock (e.g. Cook and Cole, 1991), it is unlikely that simulation models capture these differences across the landscape. Incorporation of these results into simulation models may produce important differences from current forecasts of climate change impacts on forests.

Finally, land-use history, elevated nitrogen deposition, elevated carbon dioxide and change in growing season climate have been implicated as significant factors affecting the terrestrial carbon cycle. Our results suggest that winter temperatures may have a meaningful role in the terrestrial carbon cycle of temperate regions.

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Chapter 3: Growth and Climatic Sensitivity of Northern Red Oak in the Northeastern U.S.: Placing Carbon Uptake at the Harvard Forest in a Regional Perspective

Abstract:

Carbon sequestration by oceans and terrestrial ecosystems play a significant role in atmospheric CO_2 concentrations. Eddy-flux measurements in a northern red oak dominated forest at the Harvard Forest (HF) show that it added an average of 2 tons of carbon ha^{-1} yr^{-1} from 1990-2001. Growth rates and trends of northern red oak at Harvard Forest were compared to 19 other forests dominated by northern red oak across the northeastern U.S. to understand environmental factors influencing tree growth rates. The main goal of this study is to place the growth rates of HF northern red oak in a long-term regional context. Northern red oak trees were cored, cross-dated and analyzed using standard dendrochronological techniques. Also, a new tree-ring method was developed to estimate potential site-level productivity.

In two HF plots, northern red oak growth rates over the last 50 years have been relatively steady. Gypsy moth defoliation events in 1945-1946 and1981 had a stronger impact than climate on growth rates of surviving northern red oak at annual to multi-annual time-scales. As there is no significant difference in growth rates between plots for either species after 1961, the plot adjacent to the eddy-flux tower can be considered to be representative of similar stands at the Harvard Forest over the last 40 years. There are, however, contrasting trajectories in growth rates between northern red oak and red maple

since 1992 within these stands, which suggest shifting demographics and stand composition.

The regional network shows that most northern red oak populations have increased growth rates since the 1950s with the highest growth rates occurred in the late-1970s and late-1990s to early-2001. Like at the HF, gypsy moth defoliation has the most significant impact on northern red oak growth rates and limits recovery more than climate or other non-gypsy moth disturbance events. As early-summer drought, gypsy moth and winter temperatures are the primary constraints on northern red oak growth, it follows then that regional growth rates peaked during periods of less defoliation, reduced drought and increased winter temperatures.

Harvard Forest northern red oak were among the least productive populations over the 20th century. Older northern red oak populations tend to have higher average growth rates. For example, the oldest known population, Wachusett Mountain, has a significantly higher average growth rate between 1990 and 2001 than the HF northern red oak populations. From 1977-2001 the strongest non-climatic factors correlated to northern red oak growth are average population DBH and standard deviation (SD) of population DBH. Latitude has a strong influence on the trend in growth rates between 1977 and 2001, especially after differences in site quality are removed. Old age does not apparently limit northern red oak growth rates of the 20 populations sampled. Results here suggest that old forests can be productive. The new tree-ring based index of potential productivity places the HF sites directly on the regional mean. If this new index is a good indicator of potential site productivity, the site upon which the forest around the HF eddy-flux tower plot is growing upon is typical of the northern red oak forests sampled for this study. These results suggest that the low growth rates of the HF tower plot trees are related to age and stand development. Finally, if individual tree growth rates are related to stand-level productivity, northern red oak-dominated forests in the northeastern U.S. could be sequestering significantly more atmospheric CO_2 than the forest surrounding the Harvard forest eddy-flux tower.

Introduction:

Variation in atmospheric CO_2 concentrations depends on carbon sequestration by oceans and terrestrial ecosystems (Houghton et al., 2001). Many studies suggest that mid-latitude forests are an important sink for atmospheric CO_2, possibly removing a significant amount of the global fossil fuel input (e.g., Tans et al., 1990; Keeling et al., 1996; Myneni et al., 1997; Battle et al., 2000). The locations, mechanisms, and longevity of this ecosystem function, however, remain uncertain. Therefore, understanding the factors that control CO_2 uptake by forests is critical to making predictions of future atmospheric CO_2 concentrations and the potential feedbacks into climate change.

Eddy-flux measurements at Harvard Forest (HF) are the longest continuous record of carbon exchange in a forest environment, showing an average of 2 tons of C ha^{-1} yr^{-1} added to the ecosystem (Goulden et al., 1996; Barford et al. 2001). Much of this added carbon goes directly into aboveground woody biomass of the forest, which accounts for 70% of 8-yr mean ecosystem net uptake, a typical amount for northern hardwoods (Whittaker et al. 1974). Northern red oak (NRO) (*Quercus rubra* L.) accounts for over 50% of the aboveground woody increment and is the most important contributor of carbon accumulation in live biomass. Because of its high stem density, red maple is another key species, accounting for 12-16% of the aboveground woody increment annually at the HF.

A study was initiated to understand the influence of climate and gypsy moth defoliations on NRO growth rates at the Harvard Forest and across a range of northeastern U.S. forests (Figure 1) to provide a temporal and regional context for the study of carbon sequestration as well as the factors constraining NRO growth rates at HF. A temporal and regional context will help address the following questions: "*Are growth rates of northern red oak and red maple at the Harvard Forest increasing, decreasing or relatively constant?*"; "*Are Harvard Forest NRO growth rates and trends typical for the northeastern U.S.?*"; and *"What are the important abiotic and biotic factors of tree growth rates across the region?"*

To answer these questions, growth rates of NRO and red maple at the Harvard Forest tower plot (TP) are first compared against growth rates of NRO and red maple from a nearby plot with a similar species composition, basal area and stem density (Lyford plot - LP) to determine if TP growth rates are representative of HF. Red maple is also used to characterize age structure and stand history, which will give insight to the interaction between stand dynamics and tree growth rates. The influence of gypsy moth defoliation events, a comparison of growth trajectories and the importance of climatic factors for both species are also explored at HF.

After the HF analysis, the Harvard Forest NRO populations will be compared against NRO populations across the northeastern U.S. (Table 1). A question concerning the forest around the HF eddy-flux tower is whether the responses to environmental variables are representative of northern biomes (Goulden et al., 1996). A network of 18

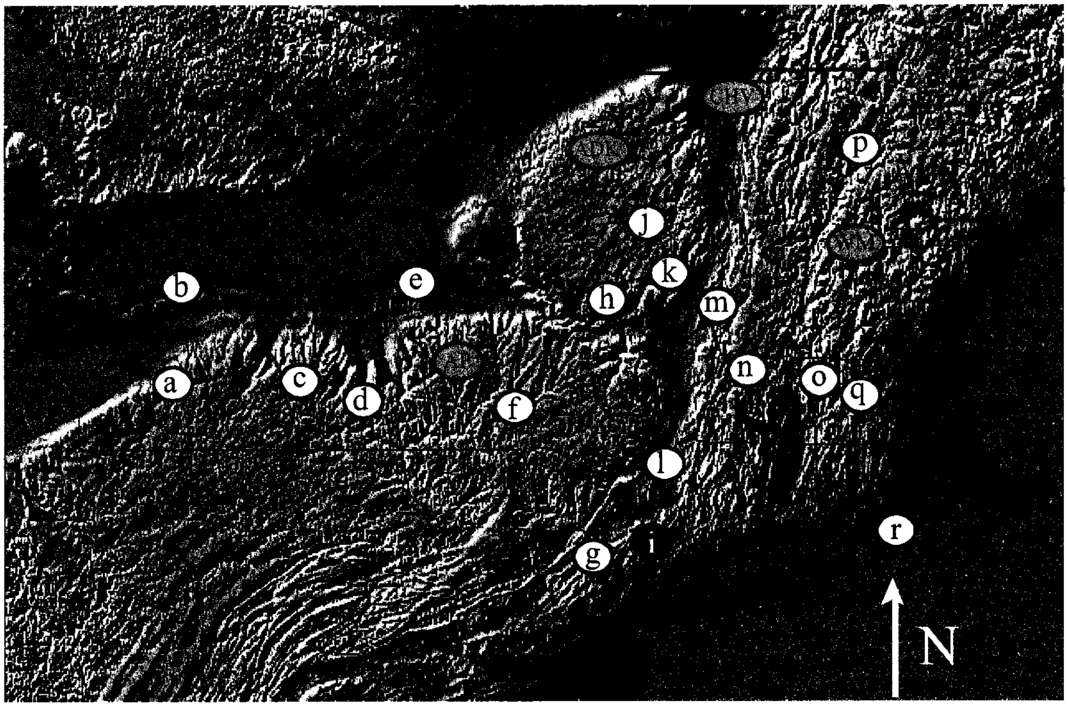

Figure 1 - Northern red oak network locations - White ovals represent locations with one population sampled. The yellow oval represents the two populations sampled at Harvard Forest (HF). The blue oval represents the two populations sampled at Black Rock Forest. From west to east populations sampled are: a) Deer Lick Preserve, Zoar Valley, Gowanda, NY; b) Singer Farm, Appleton, NY; c) Whispering Creek, Naples, NY; d) Arnot Forest, Van Etten, NY; e) Curtiss-Gale Wildlife Wildlife Management Area, Fulton, NY; f) Pine Lake Forest, Hartwick, NY; g) Uttertown, NJ; h) Rooster Hill, Caroga, NY; i) Black Rock Forest, NY; j) Goodnow Mountain, Newcomb, NY; k) Prospect Mountain, Lake George, NY; l) Montgomery Place, Annandale-On-Hudson, NY; m) Goose Egg Ridge, Cambridge, NY; n) Mohawk Trail State forest, Charlemont, MA; o) Harvard Forest, Petersham, MA; p) Sheridan Mountain, Guildhall, VT; q) Wachusett Mountain, Princeton, MA; and r) Aquidneck Island, RI. The orange ovals represent several of the physiographic provinces: AP = Alleghany Plateau, ADK = Adirondack Mountains, CHV = Champlain Valley and WM = White Mountains. The Green and Taconic Mountains and Connecticut Valley lie between the WM and CHV. The Harvard Forest lies at the northeastern edge of the broad, lower portion of the Connecticut Valley and the Berkshire Mountains lies just west this part portion of the Connecticut Valley. The Hudson Valley lies between the Berkshire Mountains and Alleghany Plateau. The Singer Farm and Curtiss-Gale populations lie within the Erie-Ontario Lowland province. Yellow to red colors represent mountainous areas while greens represent lowlands. Topographic map adapted from Ray Steiner's Colorlandform Atlas of the United States: http://fermi.jhuapl.edu/states/states.html.

Table 1 – Site characteristics of northern red oak populations sampled for this study. See text for additional descriptions and Figure 1 for spatial distribution.

Site	Location	Basal Area[1] [m^2/ha]	Sampling Density	Age Structure [years]	Average Diameter at Breast Ht.	General Land-Use History & Site Description
	Lat./ Long.	Live [Std. Dev.]	# of trees [cores]	Min.[2], max., Ave med[3], Std. Dev.[4]	[Med., Std. Dev.]	
Aquidneck Island, RI	41.569 71.284	24.0 [6.5]	21 [42]	34, 145, 96.6 103.5, 33.8	62.7 [62.4, 16.4	Not clear - a narrow ravine with evidence of an old dam on stream in ravine
Arnot For., NY	42.272 76.627	28.0 [5.5]	21 [42]	78, 117, 98.2 99.5, 11.7	59.9 [62.2, 13.0]	Second or third growth at bottom of slope; good soil development
Black Rock For. Blue, NY	41.401 74.023	-	30 [90]	55, 150, 111.8 120.0, 27.4	36.9 [35.3, 10.5]	Second or third growth on flat ridge above a stream; shallow soils; low productivity permanent plot at BRF
Black Rock For. Lucky, NY	41.407 74.039	-	30 [90]	66, 124, 84.8 84.5, 11.0	35.9 [35.0, 8]	Second or third growth at base of Mt. Misery; high productivity permanent plot at BRF
Curtiss-Gale WMA, NY	43.289 76.389	33.0 [8.1]	20 [40]	109, 177, 156.0 149.8, 17.9	75.0 [77.8, 15.8]	Wildlife Man. area along the Oswego River; no signs of disturbance in oak stand since salvaging of American Chestnut
Goodnow Mtn, NY	43.908 74.218	23.2 [8.3]	20 [40]	40, 118, 89.0 79.5, 18.0	42.6 [40.0, 11.4]	Not fully understood; on a steep, south facing slope with shallow soils; are not thought to ever have been cut
Goose Egg Ridge, NY	43.068 73.290	26.4 [3.9]	21 [36]	108, 205, 182.3 187.5, 20.7	45.1 [43.6, 8.8]	Primarily old-growth; a small section of second growth; burned in late-1800s for blueberry production
Harvard For. Lyford Plot, MA	42.530 72.183	35.3 [-]	35 [105]	74, 102, 92.1 95.0, 7.4	44.6 [45.3, 5.0]	Agricultural abandonment in late 1880s?; limited logging in early 1900s?; on slope above a wetland

Site	Location	Basal Area[1] [m^2/ha]	Sampling Density	Age Structure [years]	Average Diameter at Breast Ht.	General Land-Use History & Site Description
Harvard For. Tower Plot, MA	42.537 72.174	35.8 [-]	35 [105]	57, 107, 80.5 72.0,18.0	43.7 [40.2, 10.1]	Agricultural abandonment in late 1880s; limited logging in early 1900s; see Fig 5 for more details; flat area with shallow soils
Mohawk Trail State Forest, MA	42.061 72.301	39.8 [7.9]	21 [42]	84, 130, 104.8 103.0, 12.2	71.3 [69.6, 9.9]	Ag. abandonment in 1870s?; canopy disturbance in 1890s, 1930s; bottom of steep slope; basalt bedrock, talus in places
Montgomery Place, NY	42.011 73.921	39.0 [10.1]	20 [40]	75, 220, 138.8 135.5, 43.3	76.9 [74.8, 17.7]	Along the Hudson River; continuous forest since the early-19th century – see Pederson et al., 2004; deep soils
Pine Lake For., NY	42.471 74.926	27.0 [4.2]	20 [40]	78, 117, 98.2 99.5, 11.7	42.3 [41.2, 7.9]	Second growth, likely salvaged for American Chestnut, fire in 1908, tornado in 1984; on a shallow-soiled ridge
Prospect Mountain, NY	43.418 73.755	32.4 [10.9]	23 [33]	95^4, 188, 133.5 147.5, 36.3	49.1 [46.8, 7.7]	Disturbance in 1820s, 1890s; hotel and cable car line built in late-1800s; fire in 1910s?; shallow soils, south-facing slope
Rooster Hill, NY	43.230 74.526	36.0 [4.9]	22 [43]	86, 221, 143.9 118.5, 44.6	51.1 [51.5, 10.6]	Base of hill logged, no evidence of logging on northern slope – see Pederson et al., 2004; shallow soils
Sheridan Mtn., VT	44.528 71.638	25.5 [6.2]	21 [42]	84, 145, 108.2 106.0, 18.3	55.1 [53.3, 15.7]	Lower slope logged prior to chainsaws, upper slope partially cut more recently; shallow soil on southern slopes; presence of red spruce like Rooster Hill, NY
Singer Farm, NY	43.350 78.661	30.8 [2.9]	20 [41]	56^4, 203, 93.9 127.0, 43.6	84.9 [74.6, 29.9]	Likely a sugar bush or park in 1800s; American chestnut salvaging in 1920s; deep soils on shore of Lake Ontario

Site	Location	Basal Area[1] [m^2/ha]	Sampling Density	Age Structure [years]	Average Diameter at Breast Ht.	General Land-Use History & Site Description
Uttertown, NJ	41.117 74.417	37.5 [7.1]	20 [41]	112, 218, 157.5 144.5, 32.1	59.9 [59.4, 13.2]	Old- and second-growth forest; soils of varying depths on an undulating surface of sandstone bedrock
Wachusett Mountain, MA	42.487 71.887	35.0 [-]	39 [40]	100, 325, 224.0 205.0, 54.8	-	Old-growth; perhaps some limited firewood cutting or grazing in 1870s – see Orwig et al., 2001.
Whispering Creek, NY	42.682 77.430	41.2 [7.5]	20 [40]	86, 175, 125.7 111.9, 21.3	60.3 [58.0, 12.3]	Reportedly old-growth, perhaps some light logging on lower slopes and salvaging of American chestnut;
Deer Lick Preserve, Zoar Valley, NY	42.423 78.895	33.8 [13.9]	20 [40]	53, 142, 83.2 84.5, 21.3	59.3 [51.9, 15.1]	Flat area above valley second growth, steep slopes likely never cut, river terrace may be second-growth; soils generally shallow, though river terrace soils deeper

[1] –Trees larger than 10 cm DBH; [2] – Younger cores exist, but are rotten. Minimum tree age presented here represents first solid tree.; [3] - median age; [4] – standard deviation of population ages

additional populations outside of the HF spanning a range of climatic settings, site productivities land-use/disturbance histories is needed to provide the regional context to address this question. If the HF population is determined to be atypical of the forests sampled, then estimates of terrestrial carbon sequestration may need to be reconsidered. The regional analysis will include a study of annual carbon increment, the factors influencing NRO growth rates, the impact of gypsy moth defoliation on tree growth rates and a tree-ring based index of potential site productivity. These analyses will provide a temporal and regional context for carbon sequestration at the Harvard Forest during the 1990s and will also provide insight as to how tree growth rates in the northeastern U.S. may change in the future.

Methods:

a. Regional Geography

The region of study is geologically and geographically diverse (Figure 1). Glaciers covered the entire study region during the last glacial maximum, roughly 18,000-25,000 years ago. The eastern end of the study region is dominated by the Appalachian Highlands, which are composed primarily of the north to south running Taconic, Berkshire, Green and White Mountain formations. These mountains range up to 1910 meters in height and are composed of many different rock types including schist, marble, gneiss and granites. The Appalachian Highlands of New England are much lower in height and less rugged along the coast. Although southern New England is relatively low and flat, it is not a part of the Coastal Plain province. Other prominent north-south features in the eastern end of the study region are the broad, low-lying Hudson River, Champlain and Connecticut Valleys. The Hudson and Connecticut Valleys are rift valleys created when the North American and African continents moved away from each other 220 million years ago. Together, the Hudson and Champlain Valleys divide the study region almost in half.

The western end of the study region is dominated by three prominent features; the Alleghany Plateau, Adirondack Mountains and Erie-Ontario Lowlands. The Alleghany Plateau (AP) runs east to west along the southern end of New York State (NYS). The western end of AP is a hilly region dissected by deep, glacial valleys. The eastern end of the plateau is dominated by the Catskill Mountains, ranging up to nearly 1300 meters, which are more rugged than the hills to the west. Sandstone, limestone and shale laid down as sea sediment during the Devonian era make up most of the bedrock west of the Hudson Valley. The Mohawk Valley, an east-west river valley, separates the Adirondack Mountains from the Catskill Mountains. The Adirondack Mountains are distinct from the Appalachian Highlands in that the Adirondacks are a southern extension of the one billion year old metamorphic and plutonic rock that forms the Canadian Shield. The Adirondacks Mountains range up to more than 1600 meters in height. The Erie-Ontario Lowlands region is relatively flat, although glacial features such as eskers, potholes and drumlins make up its topography. The region has glacial till deposited over sandstone, shale and limestone bedrock.

b. Regional Climate

The climatology of the study region is nearly as diverse as the geology. Climate in the eastern end of the study region has been called “one of the most varied in the world”

(Keim, 1998; Keim and Rock, 2002). The region's climatic variability is related to its mix of mountains, low-lying large river valleys, location in the mid-latitudes and proximity to the Great Lakes and Atlantic Ocean. An interaction between the geography of North American and the region's latitude places it at the average convergence of the winter Arctic and Pacific Frontal Zones (Bryson et al. 1970) and in the path of many major North American storm tracks (Rock, 2002). Similarly, cold North Atlantic and warm Gulf Stream ocean currents meet east of Rhode Island and Massachusetts. As a result, cold, dry air masses from the north and west and warm, humid air masses from the south and east continually move across the region. These geographic and circulation patterns interact to form two distinct regional climates: a permanently humid climate with warm summers in the south and a cool temperate, subcontinental climate in the north (Brouillet and Whetstone 1993).

East of the Adirondack Mountains and eastern Catskill Mountains, winter and summer temperature and annual precipitation increases from north to south (Gajewski, 1988; SCAS 2005). Between 1971 and 2000 coastal regions received on average 1200 to 1500 mm of precipitation annually while lowlands in the north average 700-1200 mm annually (SCAS, 2005). Mountain ranges disrupt the precipitation gradient and receive between 1200 and 2400 mm of annual precipitation. Average minimum January temperatures along coastal New England range from -8.3° up to -6.1° C while in the Adirondack Mountains and northern Vermont and New Hampshire they range from -23.9° to -21.7° C. Average maximum July temperatures along coastal New England range from 26.7° up to 28.9° C while in the Adirondack Mountains and northern Vermont and New Hampshire they range from 23.3° to 26.1° C (SCAS, 2005). Running counter to the gradient of temperature and precipitation, the mean number of days with snow depth increases moving north. The number of days with snow depth greater than 10 cm between 1971 and 2000 ranged from 8-14 days along the coast and in the lower Hudson Valley to more than 84 days in the Adirondack Mountains and northern Vermont and New Hampshire (NCDC, 2005).

Climate is strongly modified by Lake Erie and Lake Ontario west of the Adirondack Mountains and eastern Catskill Mountains, especially in the Erie-Ontario Lowlands (EOL). Lake temperatures reduce maximum daily air temperatures throughout the year as well as cloud cover from spring through mid-summer. A less well-known feature of a lake-modified climate is the occurrence of a rainy season from the end of July though September. This season is characterized by rain events that can produce fairly large amounts of precipitation (NWS, 2005). The more famous aspect of a lake-modified climate is the production of severe snow events and high seasonal snowfall. For example, the highest one-year total of 1184 cm occurred in 1976-77 off the eastern end of Lake Ontario in the town of Hooker. Annual snowfall on the eastern end of each lake ranges from 250 to 510 cm/yr.

Perhaps as a result of the orientation of Lakes Erie and Ontario and in combination with the prevailing wind and storm patterns, the climate across the AP has an east-to-west concave pattern of annual precipitation and convex pattern of minimum January and maximum July temperatures. Generally, cooler temperatures and higher total precipitation occur at either end of the AP while warmer temperatures and less annual precipitation occurs between the two ends. The Arnot Forest NRO population, in the Finger Lakes region (FLR), is located in the center of this pattern (Figure 1). Climate of the EOL region is similar to the central FLR. Between 1971 and 2000 the eastern and western ends of the AP received on average 1010 to 1270 mm of precipitation annually while the FLR averages 810 to 1010 mm (SCAS, 2005). Average minimum January temperatures at the eastern and western ends of the AP range from -12.8° to -10.6° C while in the FLR and EOL these temperatures range from -10.6° to -8.3° C. Average minimum July temperatures at the eastern and western ends of the AP range from 23.3° up to 26.7° C while in the FLR and EOL they range from 26.7° to 28.9° C (SCAS, 2005). The spatial distribution of the mean number of days with snow depth greater than 10 cm between 1971 and 2000 in the western end of the study area is more variable than temperature and precipitation patterns. Generally, however, the FLR and western EOL average 21-42 days of 10 cm snow cover while the rest of the region averages 42-84 days (NCDC, 2005).

c. Harvard Forest Field Sampling

Prior to sampling at the HF, 35 previously tagged red maple and NRO trees per species in the eddy-flux tower footprint (TP) were randomly selected for coring. A bootstrapping experiment showed that 35 trees accurately captured biomass variability within 15% of the plot mean, which would help balance capturing the amount of tree variability to logistical constraints of this study, such as lab preparation and analysis. Dead trees encountered in the field were replaced with trees from an additional pool of trees randomly selected prior to coring. A second stand at the HF was selected for sampling to determine whether the TP trees were a good representation of the HF. The second plot (Lyford Plot; LP) was chosen based on having forest composition and stand density similar to TP (Tables 1, 2). The NRO were cored in late-winter 2002 while the red maple were cored in summer 2003.

Because lower boles of hardwoods are rarely a perfect circle, three cores per tree were removed with each radii 120 degrees apart. The first core was taken from what looked like the short side of each tree (Figure 2). The second and third cores were taken 120 degrees angles from the first core. Cores were taken at roughly 1.2 meters about the ground. Diameter at breast height (DBH) was recorded for each tree cored.

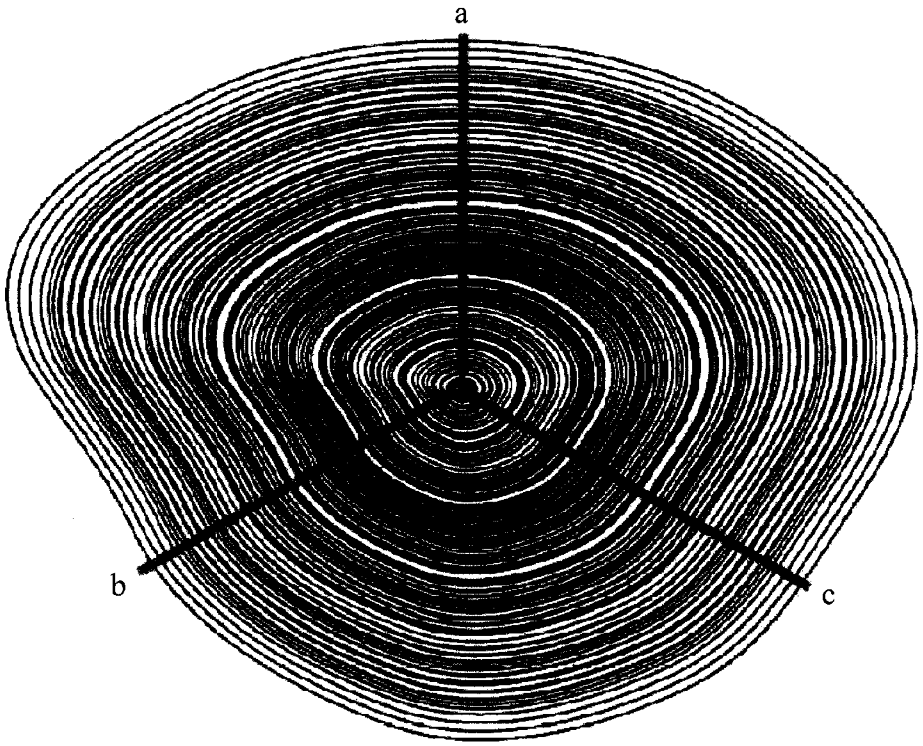

Figure 2 - Radius sampling for trees at the Harvard Forest and Black Rock Forest. Radius 'a' represents the short side of the lower stem. Radii 'b' and 'c' are set 120 degrees from 'a' to try to capture the variability in growth around the base of the tree.

Table 2 – Characteristics of the Harvard Forest red maple populations. See text for additional descriptions and Fig. 1 for spatial distribution.

Site	**Location**	**Basal Area[1]** [m^2/ha]	**Sampling Density**	**Age Structure** [years]	**Average Diameter at Breast Ht.**	**General Land-Use History & Site Description**
	Lat./ Long.	Live [Std. Dev.]	# of trees [cores]	Min.[2], max., Ave med[3], Std. Dev.[4]	[Med., Std. Dev.]	
Harvard For. Lyford Plot, MA	42.530 72.183	35.3 [-]	35 [105]	67, 111, 94.4 98.0, 12.3	17.2 [16.0, 5.9]	Agricultural abandonment in late 1880s?; limited logging in early 1900s?; on slope above a wetland
Harvard For. Tower Plot, MA	42.537 72.174	35.8 [-]	35 [105]	63, 131, 76.2 73.0, 14.3	16.6 [14.8, 5.6]	Agricultural abandonment in late 1880s; limited logging in early 1900s; see Fig 5 for more details; flat area with shallow soils

[1] –Trees larger than 10 cm DBH; [2] – Younger cores exist, but are rotten. Minimum tree age presented here represents first solid tree.; [3] - median age; [4] – standard deviation of population ages

d. New York-New England Network Field Sampling

Sites chosen for comparison to the HF NRO were based on a two primary characteristics: at least 100 yrs old and little visible stand-scale canopy disturbance over the last 50 years, such as the presence of cut stumps. After these requirements were met, sites were selected to represent a range of productivity, land-use histories and tree ages while achieving a rather even spatial distribution across southern New York State to central New England. NRO northern-range-margin populations in the Adirondack Mountains and northeastern Vermont were also targeted.

These goals were met with good success. The network includes the tallest known NRO in New England (~ 35-40 m) and a site containing the tallest known population of hardwoods in the northeastern U.S. (Mohawk Trail State Forest, MA and Zoar Valley, NY, respectively (ENTS, 2005a)), the oldest known NRO (Wachusett Mtn., MA; Orwig et al., 2001), two old-growth forests (Wachusett Mountain and Goose Egg State Forest, NY), seven old, second-growth forests (Curtiss-Gale Wildlife Management Area, NY; Montgomery Place, NY; Prospect Mountain, NY; Rooster Hill, NY; Singer Farm, NY; Whispering Creek, NY; and Uttertown, NJ), three northern-range-margin sites (Rooster Hill; Goodnow Mountain, NY; and Sheridan Mountain, VT) and three sites with climates directly moderated by large water bodies (Singer Farm; Curtiss-Gale Wildlife Management Area; Aquidneck Island, RI) (Figure 1; Table 1). Dr. David Orwig of the Harvard Forest and Dr. Ed Cook and Paul Krusic of the Tree-Ring Lab at Lamont-Doherty Earth Observatory cored the Wachusett Mountain NRO prior to this study and graciously shared their data.

Except for Black Rock Forest and Wachusett Mountain populations, trees from sites outside of HF were sampled using more standard dendrochronological methods: at least 20 overstory trees were selected for coring with two cores removed per tree. Like the HF, cores were taken at roughly 1.2 meters about the ground. At Wachusett Mountain, one core per tree was typically removed from each NRO (Orwig et al., 2001). At Black Rock Forest (BRF), 30 trees each from a high and low productivity stand each were randomly selected in the field and cored to compare long-term carbon uptake estimates from repeated measure and tree-ring data. Like the HF collection, three cores per tree were collected from BRF. When comparing HF and BRF data with the regional NRO network, 10 (BRF) and 15 (HF) understory trees were removed and one core per tree was randomly removed so that sample sizes of these populations were more similar to those from the network populations. Although not ideal, thirty-nine trees from the Wachusett Mountain population were used in this study because only one core per tree was taken. It seems important to make this exception so that the oldest population of NRO can be included in this study.

In each population forest composition and density was characterized using a forest cruise prism. The Arnot, Harvard and Black Rock Forests and Wachusett Mountain data were previously collected. At least four measurements of basal area (BA) were taken and averaged to characterize the forest. BA measurements were made at every fifth tree cored. DBH of all trees cored for this study were recorded.

e. Tree-Ring Analysis Methods

Cores were processed according to standard dendrochronological techniques (Stokes and Smiley, 1968; Fritts, 1976; Cook and Kariustis, 1990). All samples were visually cross-dated by identifying pointer years common to most trees in each population (Schweingruber et al., 1990; Yamaguchi, 1991). Cross-dating was statistically verified using the program COFECHA (Holmes, 1983). Annual ring widths were measured to the nearest 0.001 mm after cross-dating.

Because interest was in tree-level growth rates, multiple cores were averaged to create an average radius per tree. These average radii were combined into time-series of annual average ring width for each population. These time-series were used to reconstruct the annual inner-bark diameter. The reconstructed diameter represents the average stem diameter for each population. Average annual diameter was then placed into an allometric equation for northern red oak and red maple to calculate annual aboveground biomass (Ter-Mikaelian and Korzukhin, 1997). The Brenneman et al. (1978) allometric equation for aboveground biomass in Ter-Mikaelian and Korzukhin was used for both species. Average aboveground carbon increment (ACI; kg yr^{-1}) was calculated by multiplying the annual aboveground biomass by 0.498, which represents the percent of carbon per unit of biomass (Birdsey, 1992). An increment of zero was used for years when rings were missing.

f. Tree-Ring Based Site Productivity: Realigned Aboveground Carbon Increment

i. Rational for Methodology

Preliminary ACI analysis indicated that older populations tended to have higher growth rates. Therefore, a new method of estimating potential site productivity, akin to the tree-height based site index used in forestry, was developed based on radial increments. The new index is then used to determine the relative rankings of site productivity regardless of tree ages. The method is partially based on the principals of regional curve standardization (RCS) (Briffa et al., 1992). RCS re-aligns time series of radial increment by cambial age to estimate a mean, stand-level biological growth curve. In closed canopy forests, changes in tree-to-tree competition strongly influences growth rates, especially in trees that have not ascended to the canopy layer (i.e. seedlings, saplings, suppressed and intermediate trees). The main goal of the methodology below is to remove the potential time-related factors of growth (i.e., age, climate) to determine potential site productivity.

Because potential site productivity is of interest, it was necessary to reduce the influence of growth prior to canopy accession. An estimate of potential site productivity in a closed-canopied forest was achieved by examining each time series for a step change increase in growth, which is evidence of a release from canopy suppression. A traditional methodology of determining release from canopy suppression involves the identification of average rings widths over a 15-year period at least 50% and 100% larger than the prior 15 years (Lorimer and Frelich, 1989). The 50% and 100% increase in average ring widths are thought to represent minor and major growth releases, respectively. A modification of Nowacki and Abrams (1997) method by Dr. Ed Cook was used for this study. The new method, available in the latest version of the ARSTAN standarization program, allows researchers to use the time window and threshold triggers of the traditional method together with the calculation of a local standard error in ring width so that canopy disturbance events can be determined more objectively.

ii. Detecting Disturbance in Northern Red Oak

While cross-dating the Curtiss-Gale NRO it became obvious that most trees in the forest experienced a significant increase in radial growth between 1923 and 1928 (Figure 3). The presence of American chestnut (*Castanea dentate* Marsh.) sprouts in the forest and a discussion with a historian for the city of Fulton, NY led to the conclusion that American chestnut was an important component of the stand and likely salvaged (Sean Faban, personal communication). As the Curtiss-Gale population had strong evidence of a significant canopy disturbance event, it was used to determine the best thresholds for detecting disturbance in NRO with the Cook-modified method. A 75% increase in average ring width over a 12-year period with a 3 standard error limit threshold was chosen as an indication of canopy accession for this study. Disturbance detection was performed on the averaged radius for each tree.

iii. Development of Realigned Aboveground Carbon Increment (RACI)

To first develop RACI, growth prior to each identified disturbance event is removed from each time-series. In the few cases where more than one disturbance was detected, growth prior to the last disturbance event was removed. In a few rare cases this left only 20-30 years of radial growth on 80 to 120 year old trees. Radial increments for all trees were realigned so that the first year post-disturbance is year one even though the tree may be more than 100 years old (Figure 3). The realigned ring widths were averaged to create

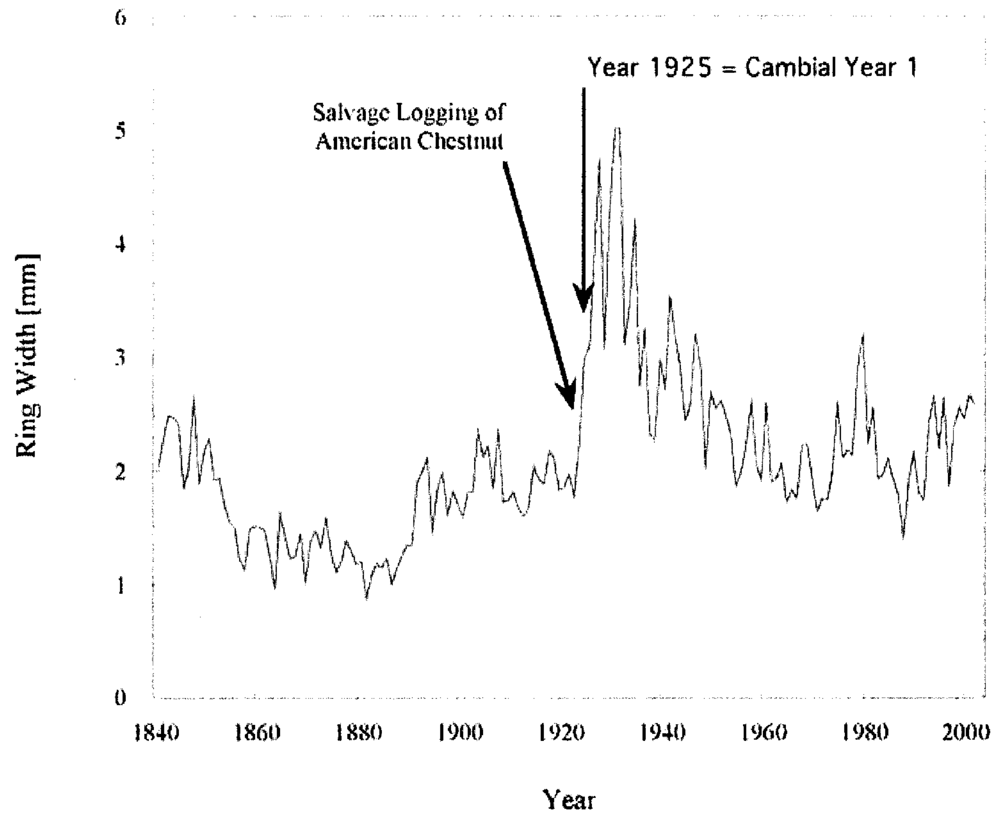

Figure 3 - Radial Growth Release Event Resulting from Canopy Disturbance: Raw radial increments of tree CGR-05 from the Curtiss-Gale Wildlife Management Area are shown above. Growth prior to 1925 is on average less than 2.0 mm/yr. Field evidence and historical account suggest that American chestnut was likely logged in this stand in the early-1920s. A significant increase in radial increment was detected by the Cook-modified disturbance detection method beginning in 1925. To estimate site productivity based on radial increments in the absence of canopy suppression, growth prior to 1925 is removed with the subsequent rings realigned to be cambial year one. Therefore, 1925 A.D becomes year one for this tree.

a time-series of post-canopy accession ring widths for each population. Ninety-five percent confidence limits of the realigned radial increments were also calculated for each population (Cook, 1990). The realigned raw ring width time-series was then placed in the NRO allometric equation described above to calculate average aboveground carbon increment. The realigned aboveground carbon increment time-series (RACI) represents maximum potential growth rates of post-canopy accession trees for each site.

Although this methodology does not likely remove all competitive effects, it does reduce, if not eliminate the influence of overstory competition prior to canopy accession. This method does not remove the influence of changes in the competitive environment once a tree has gained canopy status. Detecting these types of changes, however, is difficult in detecting (Nowacki and Abrams, 1997). Realignment of radial growth also reduces the influence of climate change through the averaging of climate-related growth from different eras so that the resulting growth curve may be more of a pure site productivity index. An exception to the reduction of climatic influence on RACI would be a site where most trees experienced a disturbance within a year or two of each other, such as the Curtiss-Gale population. The BRF Lucky Streak Red and HF Lyford Plot populations became more even-aged after removal of suppressed growth, but not as much as Curtiss-Gale. The impact of climate on growth rates of Curtiss-Gale trees over the last 80 years is still likely to be in its RACI time-series. Similarly, old populations with less significant disturbance events like Curtiss-Gale, such as Goose Egg, Wachusett Mountain or Uttertown, will have growth in the earliest part of the RACI index more influenced by pre-20th century climate. While the RACI index may not be a perfect index of site productivity, the removal of suppressed growth reduces the influence of overstory competition, tree age and climate.

In the development of RACI it became clear that an index represented by fewer than 10 trees is less stable. Therefore, only the first 70 years of post-canopy accession growth is discussed. Growth rates through 80 years are presented because many of the conclusions for the first 70 years hold true although sample replication becomes quite low for several populations, such as the HF populations.

g. Climate Sensitivity Analysis

Climatic sensitivity analysis was conducted on the combined HF NRO oak and red maple populations and then again on all NRO populations. HF populations were combined to improve sample replication, reduce potentially spurious relations or relations related to differences in stand density/competition (Cescatti and Piutti,1998*)*. There were some differences between populations at HF, although these differences were not substantial.

NRO populations were correlated to the nearest meteorological station available from U.S. Historical Climatology Network data set (Easterling et al., 1996) (Table 3). The last year of corrected data from this network is 1994. Because 1) more than half of the Tower Plot NRO were recruited into the forest between 1920 and the early 1930s, 2) there was a significant canopy disturbance at Curtiss-Gale in the 1920s and 3) Great Barrington, MA meteorological data begins in 1929, the period of correlation between climate and tree growth is 1930-1994. An exception to this period is made for the Curtiss-Gale NRO population. This population is within 15 miles of Lake Ontario and a strong band of lake-moderated climate. The nearest station within this band is the Oswego, NY, which has data available up to 1989. A meteorological station with a longer time-series of data is available from Syracuse, NY, but correlations between it and the Curtiss-Gale population are poor. Therefore, the period of climatic analysis for the Curtis-Gale populations is 1930-1989.

Residual ring index chronologies were correlated versus pre-whitened meteorological data. It is necessary to remove autocorrelation as it can make statistical modeling, hypothesis testing and data interpretation difficult (Cook, 1985). Pre-whitening is the statistical removal of autocorrelation. The meteorological data was pre-whitened from 1929 to 1994. The residual ring index chronology has the lowest amount of autocorrelation of the common tree-ring indices. Tree ring indices were correlated against average monthly minimum and maximum temperatures and total monthly precipitation over a 19-month window (prior-March through current growing season September). Tree physiology can produce a lag between the influence climate and radial growth increments (Fritts, 1976; Kramer and Kozlowski, 1979; Cook and Kairiukstis 1990).

Table 3 – List of NRO populations and the meteorological station used for climatic analysis.

Site	**Meteorological Station**	**Approximate Distance Between Site & Station**
		-- km --
Aquidneck Island, RI	Providence, RI	36
Arnot For., NY	Ithaca, NY	28
Black Rock For. Blue, NY	West Point, NY	9
Black Rock For. Lucky, NY	West Point, NY	9
Curtiss-Gale WMA, NY	Oswego, NY	17
Goodnow Mtn, NY	Indian Lake, NY	22
Goose Egg Ridge, NY	Gloversville, NY[a]	79
Harvard For. Lyford Plot, MA	Amherst, MA	30
Harvard For. Tower Plot, MA	Amherst, MA	30
Mohawk Trail State For., MA	Great Barrington, MA[b]	63
Montgomery Place, NY	Mohonk, NY	34
Pine Lake For., NY	Cooperstown, NY	29
Prospect Mountain, NY	Gloversville, NY[a]	66
Rooster Hill, NY	Gloversville, NY[a]	15
Sheridan Mtn., VT	St. Johnsbury, VT	39
Singer Farm, NY	Brockport, NY[b]	59
Uttertown, NJ	Port Jervis, NJ	36
Wachusett Mountain, MA	Clinton, MA	16
Whispering Creek, NY	Geneva, NY[b]	44
Deer Lick Preserve, Zoar Valley, NY	Fredonia, NY[b]	33

[a] – The Gloversville station is the best station suited for climatic analysis based of distance to nearest meteorological station and elevation (also see Pederson et al., 2004). [b] –the closest station with the fewest missing data.

Results/Discussion:

Comparison of Tower and Lyford Plot Northern Red Oak and Red Maple at the Harvard Forest:

a. Cross-dating:

All cores needed to be cross-dated before age structure and disturbance history could be accurately produced. Cross-dating proved to be most difficult and most necessary for red maple. A large gypsy moth outbreak in 1981 in central and southern New England (USFS, 2003) resulted in narrow latewood widths in NRO and "white rings" in red maple (Figure 4a). The narrow rings and white rings acted as pointer years for both species. Formation of white rings in aspen, a diffuse-porous species like red maple, is the result of early growing-season defoliation, which produces xylem with significantly lower density in defoliated trees than non-defoliated trees (Hogg et al., 2002b). Given that red maple is palatable to gypsy moth (Liebhold, 1995), the intensity of the 1981 event, the presence of white rings in HF red maple and the relation between white ring formation and defoliation in aspen, it is safe to conclude that the HF red maple were defoliated in 1981. Despite the utility of white rings in red maple for cross-dating, it was necessary to use traditional cross-dating methods because defoliation does not appear to have been consistent between plots. Only 17% of the TP red maple cores had a white ring versus 76% of the LP cores. Important narrow pointers rings for red maple at HF were: 1938, 1945, 1959, 1966, 1968, 1970, 1973, 1981, 1988, 1996 and 1999. The combination of white rings and pointer years were especially useful because many red maple trees had extremely narrow rings or 1-12 missing rings over the last 15 years (Figure 4b; Table 4). Although correlations were low between NRO and red maple (combined species chronologies interseries correlation = 0.325, $p < 0.001$), COFECHA statistically verified the cross-dating of red maple.

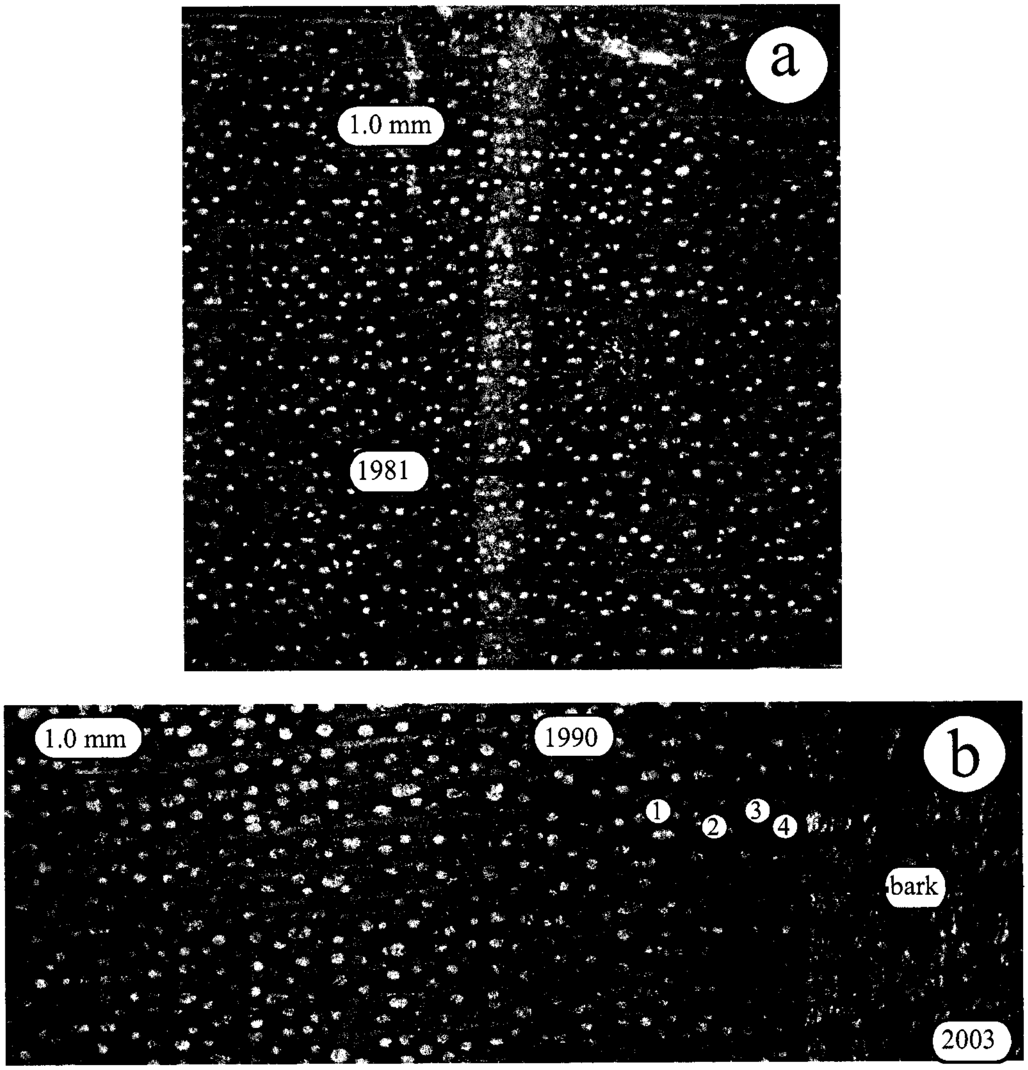

Figure 4 - White and Locally Absent Rings in Red Maple at the Harvard Forest: a) Close up of a white ring caused by the 1981 gypsy moth defoliation event. b) Radial increment growth of red maple B3204 from the Tower Plot in the 1990s. There are only four growth bands apparent between 1990 and the inner bark. This tree was alive at the time of sampling, which was in July 2003. Therefore, there ought to be 12 bands of growth between 1990 and the inner bark.

Table 4 - Locally absent ring (LAR) frequency in red maple at the Lyford and Tower Plots at the Havard Forest, MA.

	Cores with LAR	Average Number of LAR	Maximum Number of LARs
	--number--	--per core--	--per core (SD)--
Lyford Plot	31	2.6	9 (2.4)
Tower Plot	49	4.7	12 (3.2)

b. Age Structure:

The Tower Plot NRO has three age cohorts: the mid-1890s, early-1930s and late-1930s to early-1940s (Figure 5). The presence of pith in nearly half of the trees from each cohort indicates that age at coring height is distinct from the previous cohort. It is possible that trees from the youngest cohorts recruited at the same time as the first cohort, but were delayed in reaching coring height as a result of local competition or local productivity differences. The Lyford Plot NRO has two cohorts, one dating to the early-1900s and a second dating to the early-1920s. The early-1900s cohort dominates the age structure. There might be a third cohort as many NRO with pith dates were recruited into LP between the two cohorts. Splitting out this group as a third cohort may not be correct. The disturbance that triggered recruitment of the first cohort could have been the trigger for the trees with pith dates late in the1900 decade. Differences in the time to reach coring height following the disturbance may reflect differences in local growth rates. LP population has a higher average and median population age and a lower standard deviation (SD) of tree ages than the TP population (Table 1).

Red maple in each plot generally reflects the same recruitment pattern as NRO (Figure 6). The TP has two age cohorts and a single old tree. The oldest tree dates to 1872 at coring height. The first cohort dates to the late-1890s and early-1900s. The last cohort

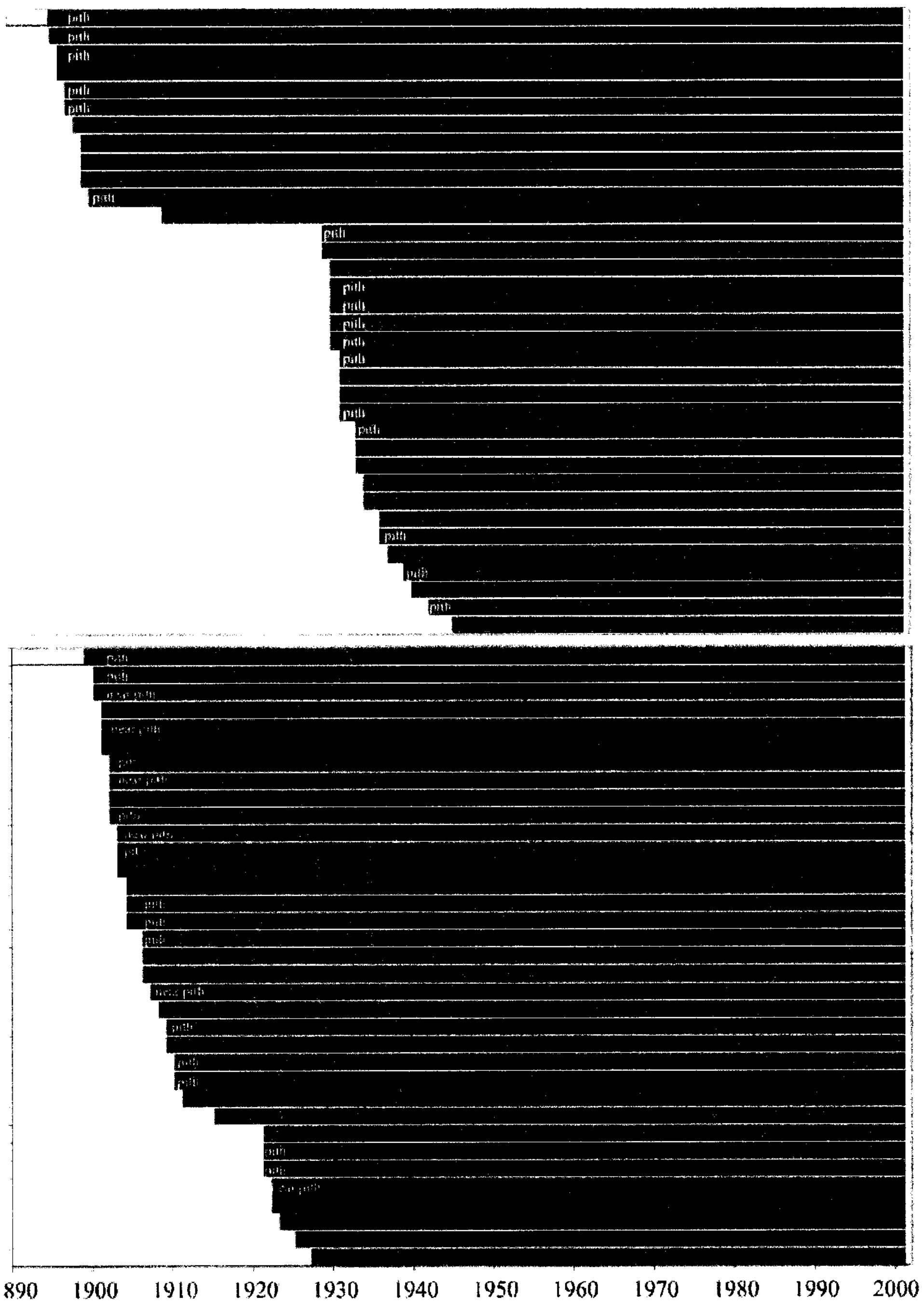

Figure 5 - Age structure of northern red oak in the Tower Plot (upper plot, red bars) and Lyford Plot (lower plot, purple bars). Each bar represents a sampled tree. The left side of each bar represents the date each tree reached coring height (~1.2 m) while the right side of the bar represents the date of coring. 'pith' indicates that at least one core per tree has the pith present. 'near pith' indicates one core that is within 1-2 years of the pith.

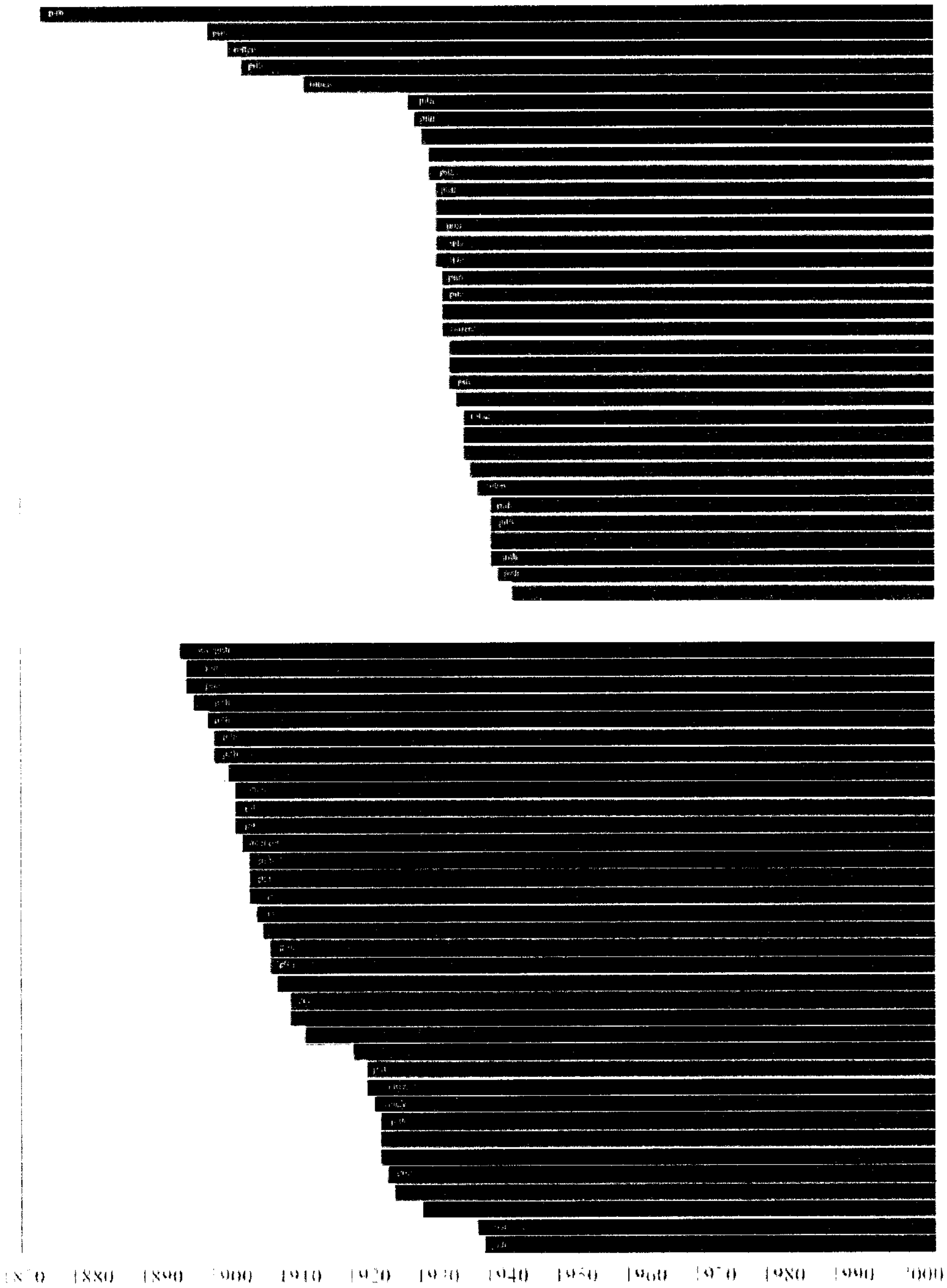

Figure 6 - Age Structure of Red Maple in the Tower Plot (upper plot, red bars) and Lyford Plot (lower plot, purple bars). The left side of each bar represents the date each tree reached coring height while the right side of the bar represents the date of coring. 'pith' indicates that at leas one core per tree has the pith present. 'near pith' indicates a core that is estimated to be within 1-2 years of the pith. 'rotten' indicates a hollow tree.

dates firmly to the mid-1920s and early-1930s. Red maple in the LP has three age cohorts. There is nearly continuous recruitment at coring height between the early-1890s and late-1900s during which 62.8% of all trees sampled reached coring height. A second cohort recruited between the late-1910s and mid-1920s. Two trees were recruited in the late-1930s. LP red maple population has a higher average and median tree age than TP population (Table 2).

Tower Plot Stand History/Age Structure Discussion:

Tower Plot age structure and standardized ring widths of NRO and red maple corroborate its known land-use history while simultaneously illustrating the interaction between land-use and forest dynamics (Figure 7). Most of the TP forest regenerated following agricultural abandonment (Harvard Forest Archives). One section, nearly a third of the plot in area, was used as a woodlot. The last date of agricultural abandonment is 1908. There was considerable cutting between 1890 and 1895 (Harvard Forest Archives). This cutting led to an initial pulse of tree recruitment in both species. The presence of tree pith within a few years of each other during this decade reveals that canopy density was abruptly reduced and the advance regeneration of both species responded simultaneously. The oldest red maple tree also shows a step-change increase in ring indices just prior to this pulse of recruitment, as would be expected of a tree experiencing reduced canopy competition.

Records show considerable forest management, called ‘weeding’ in historical documents (Harvard Forest Archives), from 1925-1934 in the TP area. Continuous recruitment during this period in the TP reflects the forest management. There is an

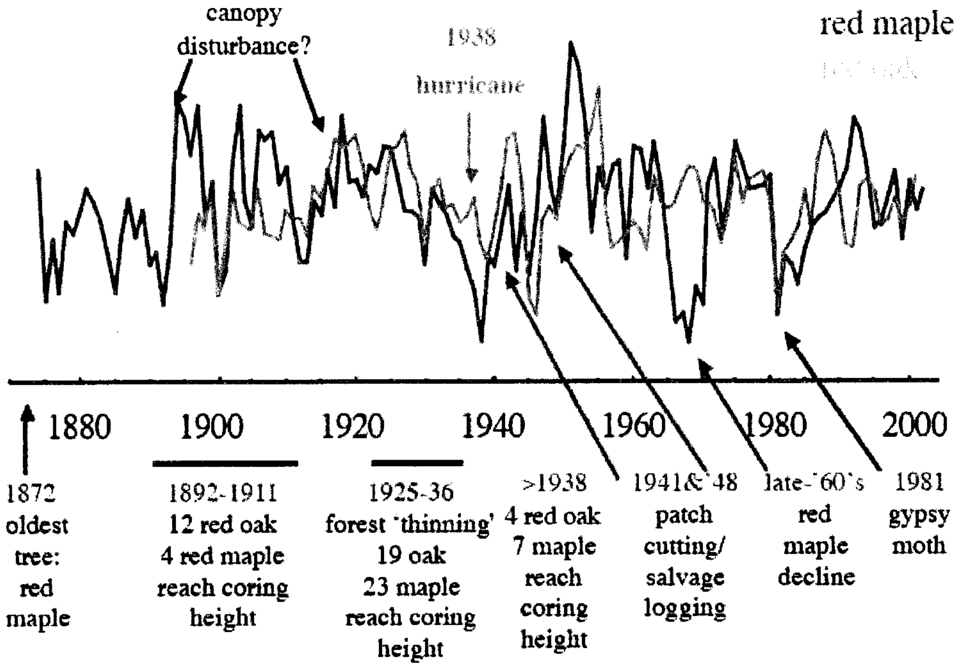

Figure 7 - Timeline of Stand History at the Harvard Forest Tower Plot: Events on this time scale are derived from tree-rings and recorded in HF Archives. The gold line is the standardized northern red oak ring index. The red line is the traditional standardized red maple ring index. Black arrows indicate unknown disturbance events in the first half of the record and the 1981 gypsy moth defoliation event. The 1938 Hurricane is noted with the orange arrow. The green arrows show cutting events. The red arrow indicates the red maple growth decline.

increase in radial growth of NRO and red maple in 1918 that is not easily explained as it pre-dates the 1920-1930 era of stand management. Age structure supports historical documents showing that most of the TP experienced only 'very slight damage' (<10% canopy damage) as a result of the 1938 hurricane. Roughly 20% experienced 'severe' damage (76-100% canopy damage) following the 1938 hurricane with a smaller amount experiencing 'moderate' damage (25-50% canopy damage). Only a minority of trees in a small portion of the stand grew to coring height following 'weeding' in 1938 and salvage logging in 1941. The small number of trees recruited after the hurricane suggests that a high stem density in the advanced regeneration or sapling layers did not allow the recruitment of new trees. A forest type map from 1923 shows a dominance of grey birch, suggesting that the stand was in a successional state prior to the hurricane. This evidence supports records indicating the Tower Plot is pre-1938 Hurricane forest.

Heavier forest management, like 'thinning', 'salvaging' and 'improvement', occurred in 1948 throughout the stand. Growth rates of TP trees reflect this disturbance. The only other notable events in the TP are the red maple growth decline in the late-1960s and gypsy moth defoliation events in 1945-46 and 1981. The combination of tree-ring data and historical documents show how alterations of the forest canopy triggers changes in growth and recruitment of trees into the stand at coring height.

Tower Plot Versus Lyford Plot NRO and Red Maple Growth Rates

Average aboveground carbon increment of NRO has been relatively steady in both Harvard Forest plots since the 1950s, although TP growth rates have a non-significant upward trend and LP growth rates have a non-significant downward trend (Figure 8a). TP ACI peaked in 1988 while LP peaked in 1975. There is no significant difference in growth rates between the two stands. Wider bootstrap confidence limits around the Tower Plot NRO ACI curve shows that tree growth rates are more variable in TP than for LP rates.

Red maple ACI increased in both plots in the first half of the 20th century. Growth rates of the TP population peaked in the late-1940s while the LP trees peak and in 1970s (Figure 8b). There are significant differences in growth rates between TP and LP red maple. TP growth rates are higher than LP rates from 1931-1961 (except for 1938, 1947, and 1959), after which there is no significant difference.

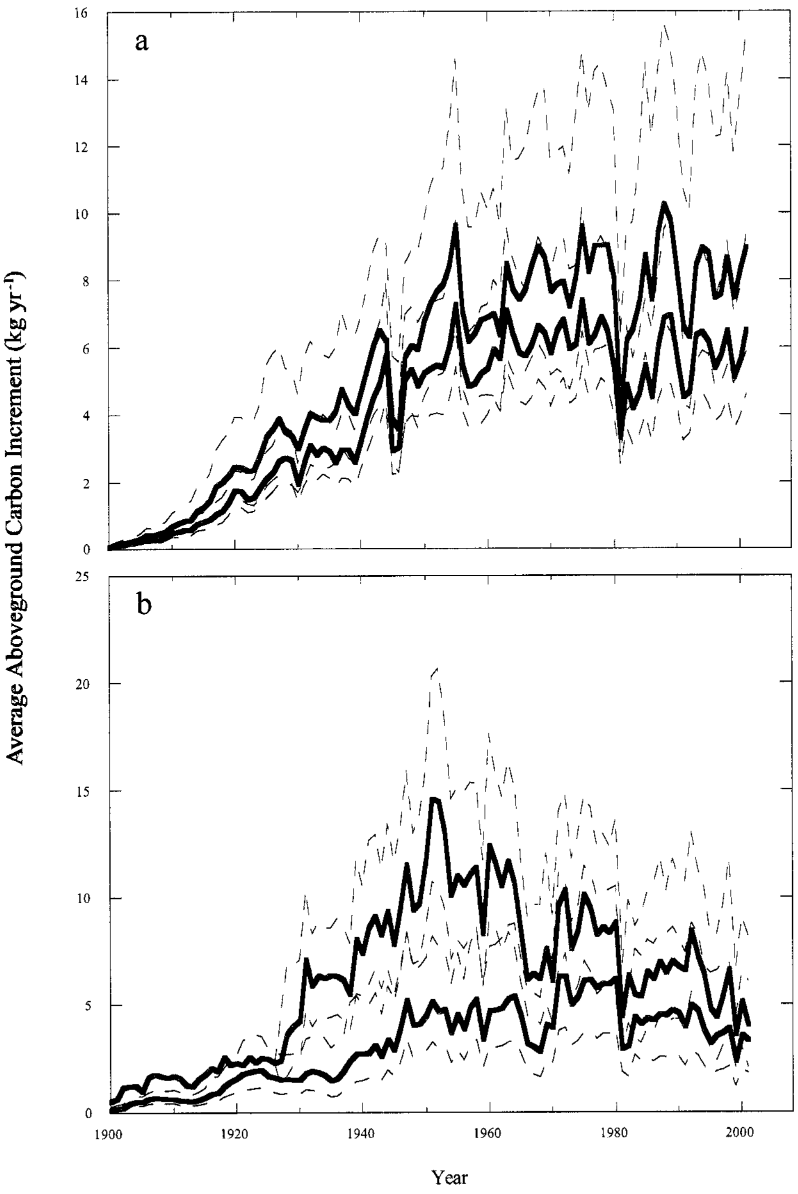

Figure 8 - Comparison of Growth Rates Between Lyford and Tower Plots at the Harvard Forest: a) northern red oak, b) red maple. Red lines represent Tower Plot in both graphs while blue lines represent the Lyford Plot. Dashed lines represent 95% confidence limits for both populations

a. Species-level Differences in Growth Rates at the Harvard Forest

Although there are no significant differences in growth rates since 1920 between NRO and red maple in both plots (Figure 9), there are differences in productivity and trends in growth rates. NRO is 26.65% and 43.96% more productive than red maple in the Tower Plot from 1977-2001 and 1992-2001, respectively (Table 5). In the Lyford Plot, NRO is 32.08% and 57.53% more productive for the same periods, respectively. Red maple has been slower to recover following the 1981 gypsy moth defoliation event than NRO. Most importantly, there are contrasting trajectories in growth rates between species, especially from 1992-2001 (Table 5). Growth rates of NRO in both plots from 1992-2001 and 1977-2001 have a weak, but non-significant upward trend in annual growth rates. In contrast, red maple has significantly negative trends from 1992-2001. Northern red oak is more productive on a per tree basis than red maple and is not experiencing the decline in growth rates since 1992 like red maple.

Differences in growth rate trends between species are most dramatic in the TP. NRO has the strongest positive trend for both periods of analysis while red maple shows the strongest negative trends (Table 3). Underscoring this difference is that six red maple trees, 17.1% of the sample, added less than 0.20 cm inner bark DBH (iDBH) at coring height between 1992 and 2002. Fifteen red maples, 42.8% of the sample, added less than 0.50 cm of iDBH over the same time period while 24, 68.6% of the sample, added less than 1.0 cm of iDBH. In contrast, all but one NRO added more than 0.20 cm of iDBH at coring height since 1992. Only one NRO, 2.8% of the sample, added less than 0.50 cm iDBH over the same time period while 4, 11.4% of the sample, added less than 1.0 cm of iDBH.

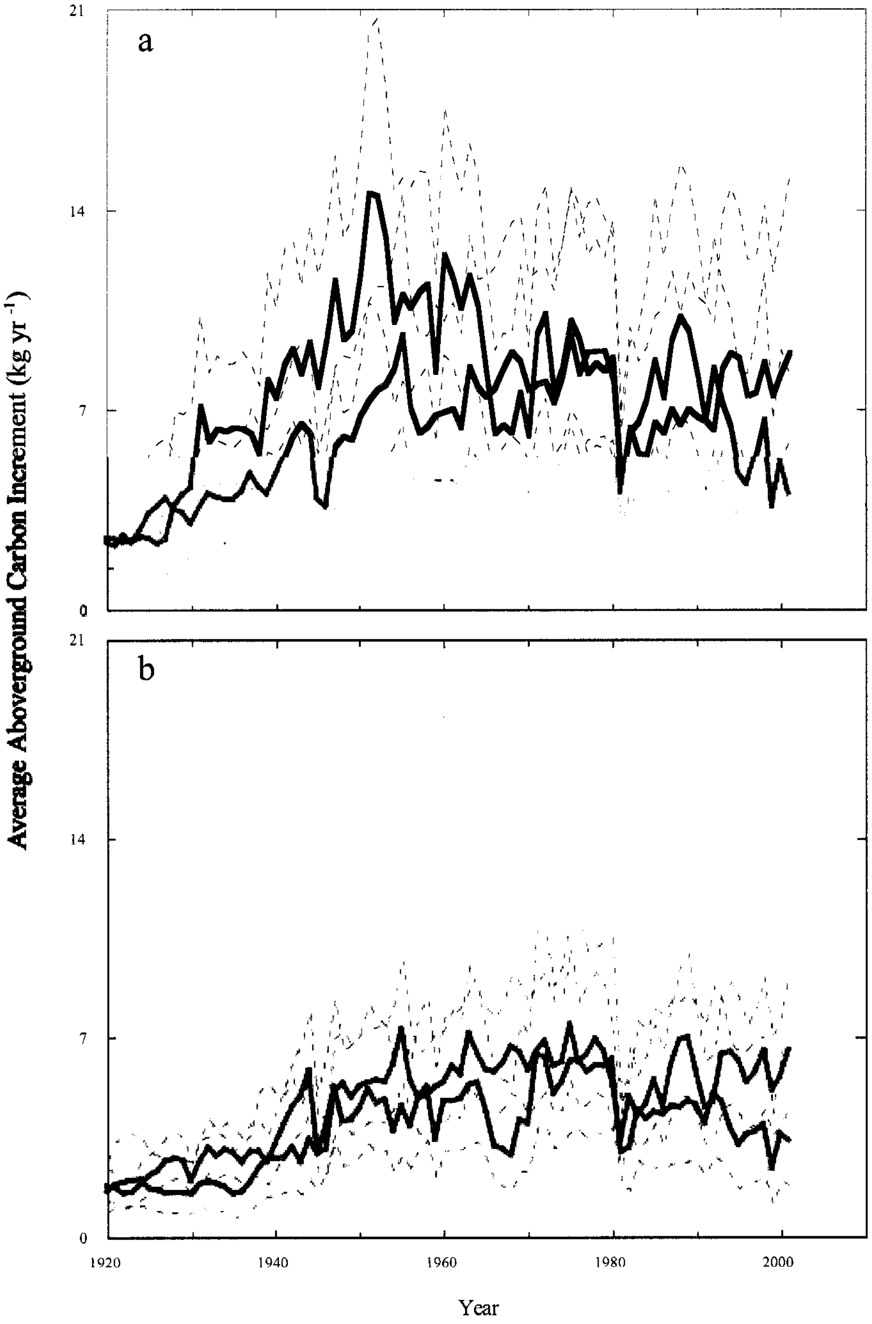

Figure 9 - Comparison of Stand-Level Northern Red Oak and Red Maple Growth Rates at the Harvard Forest: a) Tower Plot, b) Lyford Plot. Red lines in both graphs represent northern red oak growth while blue lines represent red maple. Dashed lines represent 95% confidence limits for both species.

Table 5 - Average and trend in growth rates for northern red oak and red maple from 1977-2001 and 1992-2001 at the Harvard Forest, MA. Significant trends in growth are in bold and indicated by: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Numbers in parentheses equals the correlation in trend.

	1992-2001	1977-2001	1992-2001	1977-2001
	-- Average kg carbon/year --			
	-- Northern Red Oak --		-- Red Maple --	
Lyford Plot	5.86	5.64	3.72	4.27
Tower Plot	8.09	8.03	5.62	6.34
	-- Trend in kg carbon/year (correlation) --			
Lyford Plot	0.035 (0.162)	0.021 (0.159)	**-0.168 (0.689)***	**-0.084 (0.626)*****
Tower Plot	0.093 (0.326)	0.021 (0.113)	**-0.373 (0.734)****	**-0.116 (0.582)****

b. The Influence of Gypsy Moth on Growth Rates

The 1981 gypsy moth defoliation event caused a significant downward spike in ACI in NRO and red maple. Since 1940 only the gypsy moth defoliation events of 1945-1946 produced significantly lower growth rates in surviving NRO than the 1981 event (Figure 10a, b). Growth rates were significantly higher than the 1981 event by 1987 in the LP and 1988 in the TP. Combining the growth rates of both plots indicates that growth over much of the last 50 years was significantly greater than the 1981 event (Figure 10c).

The 1981 defoliation event also had a strong impact on red maple growth rates (Figure 11a, b). TP red maple growth rates were significantly greater than the 1981 event for most of the period between 1946 and 1965. Growth rates of the LP red maple prior to 1981 were not significantly different than the 1981 event. Growth rates in both stands increased after 1981 until 1992. The average 1999 ACI value of both plots was significantly lower than the 1981 event, which further attests to the considerable decline of red maple growth rates since 1992 (Figure 11c).

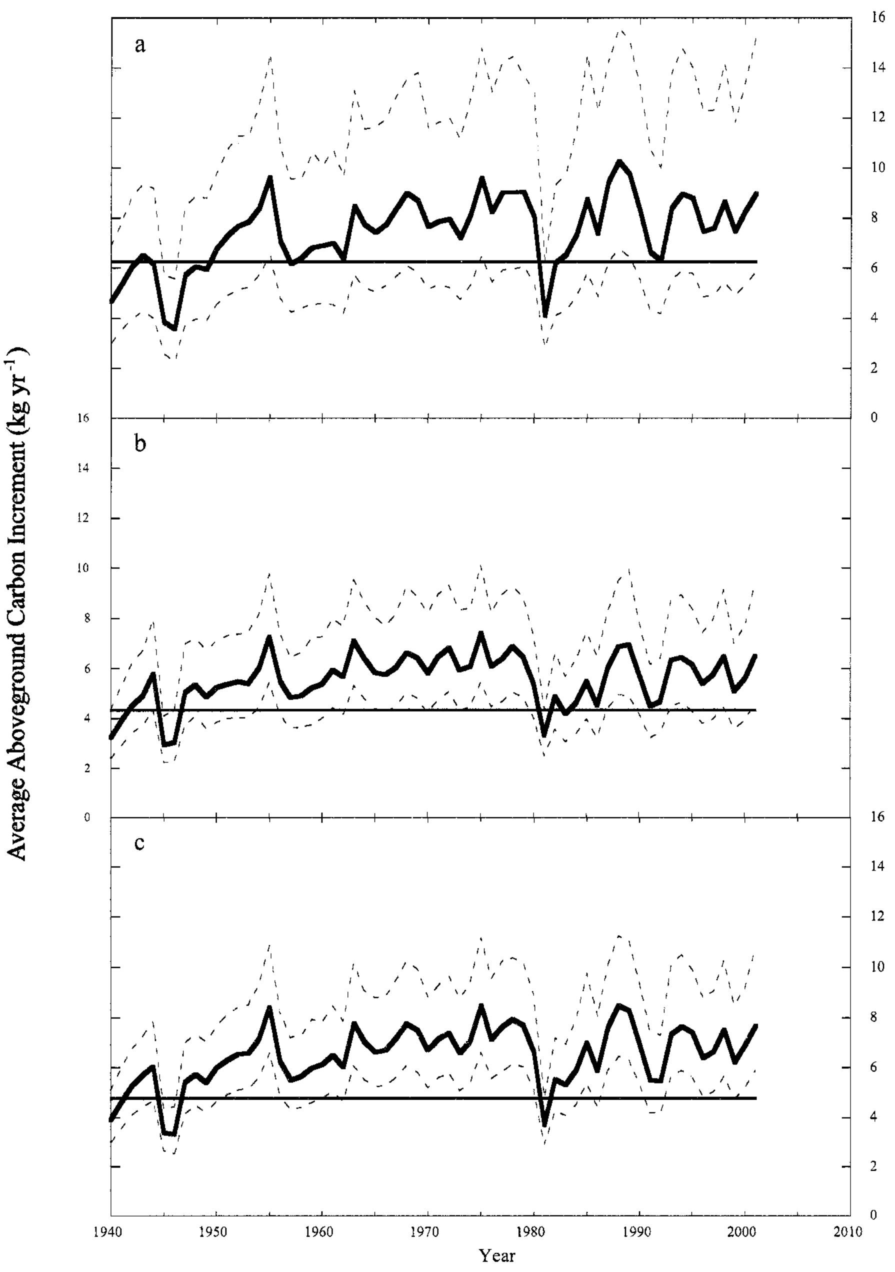

Figure 10 - Impact of Gypsy Moth Defoliation on Northern Red Oak Growth Rates at the Harvard Forest: a) Tower Plot, b) Lyford Plot and c) average of both HF plots. The blue line represents the value of the upper 95% confidence limit for the 1981 gypsy moth defoliation event for each population. Dashed lines represent 95% confidence limits.

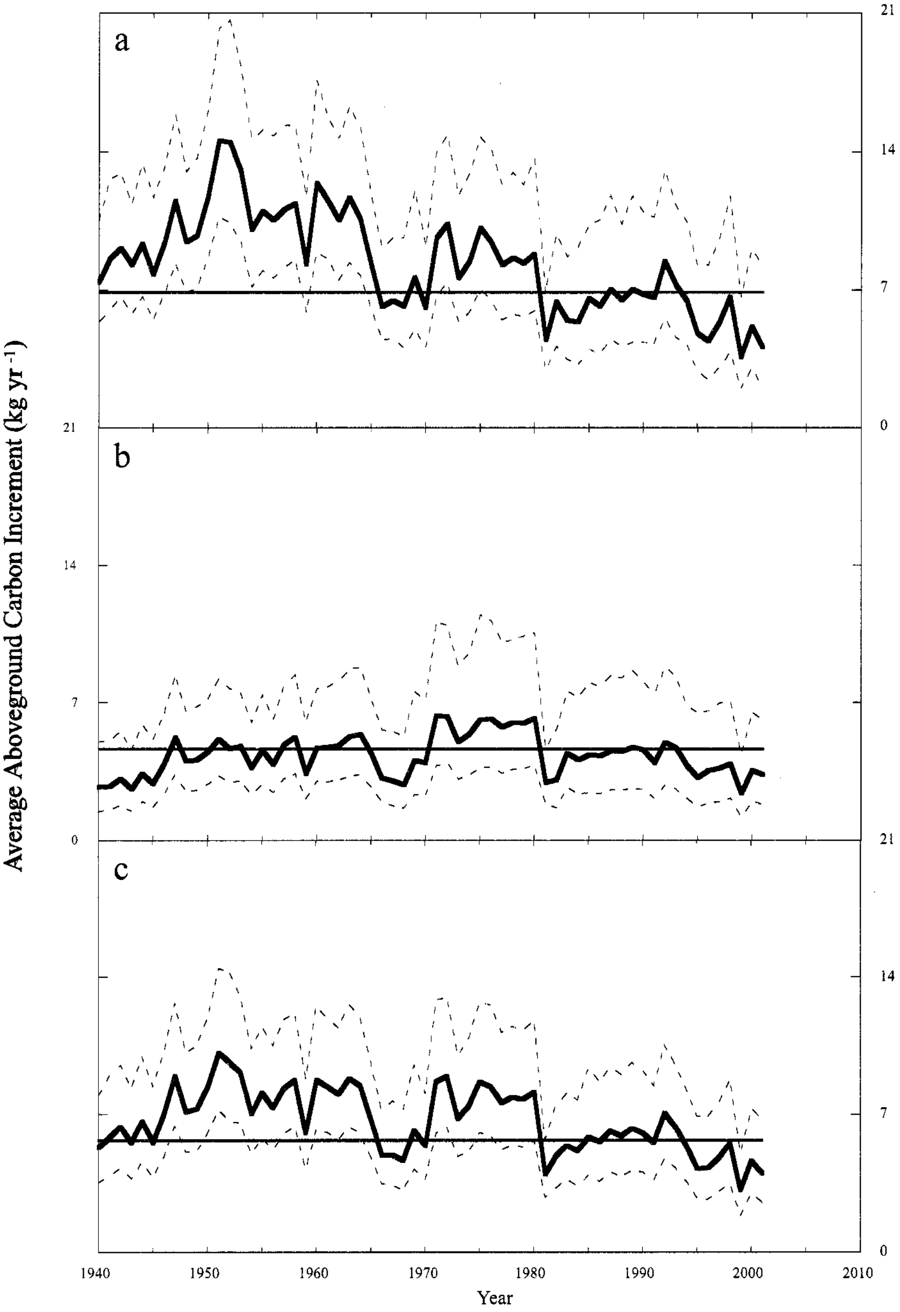

Figure 11 - Impact of Gypsy Moth Defoliation on Red Maple Growth Rates at the Harvard Forest: a) Tower Plot, b) Lyford Plot and c) average of both HF plots. The blue line represents the value of the upper 95% confidence limit for the 1981 gypsy moth defoliation event for each population. Dashed lines represent 95% confidence limits.

c. *The Influence of Climate on Radial Increment*

Precipitation has mostly a non-significant relation to the radial growth of Harvard Forest NRO and red maple between 1930 and 1994 (Figure 12a, b). NRO has a very

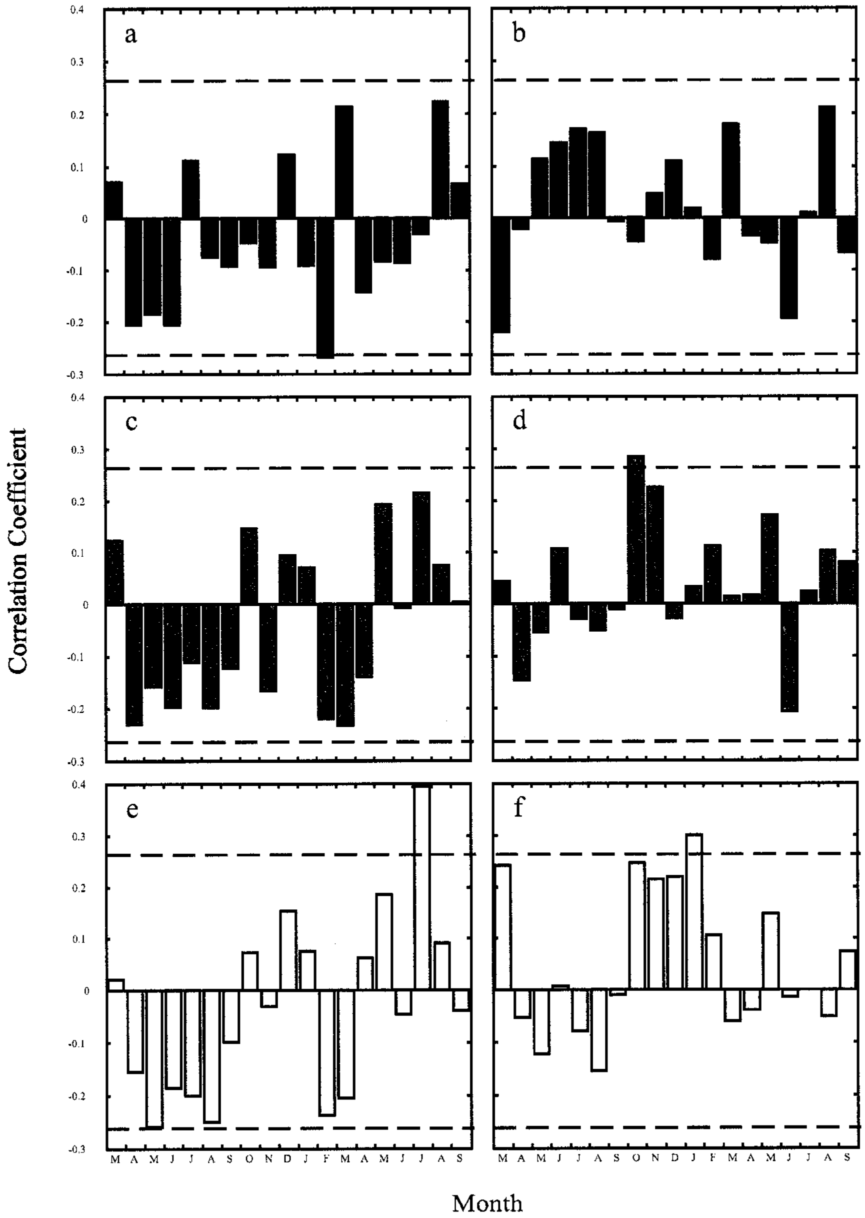

Figure 12 - Climate Correlations Between Harvard Forest Northern Red Oak (a, c, e) and Red Maple (b, d, f). Tree-ring indices are correlated versus total monthly precipitation (a, b), average monthly minimum temperatures (c, d) and average monthly maximum temperatures (e, f). Dashed gray lines indicate significant correlations at the p = 0.05 level.

unusual negative correlation to total February precipitation prior to the current growing season. Both species are more sensitive to variations in monthly temperatures (i.e., having more annual variance explained by temperature than precipitation), with red maple more sensitive than NRO (Figure 12c-f). Cool prior October minimum temperatures and cool January maximum temperatures significantly limit red maple radial growth. Average maximum temperatures from prior October through January account for more variation in red maple increment than January alone (r^2 = 15.2% vs. 9.0%, respectively). There is little difference in explained variance of prior October minimum temperatures versus average prior October and November minimum temperatures (r^2 = 15.0% vs. 11.9%). Cool July maximum temperatures limit NRO growth the most across the NY/NE study area, which is different than the findings in a study limited to the Hudson River Valley (Pederson et al., 2004; Chapter 2).

Synthesis of Tree Growth at the Harvard Forest

TP and LP NRO had relatively steady growth rates over the last 50 years, although TP rates have been increasing slightly over this period. Many red maple trees in both stands have nearly ceased radial growth increment from 1992-2002. Contrasting trends of growth rate trends suggest red maple may become less important in the future, which is a trend noted from permanent plot data at the Harvard Forest (Rockwell, 2004). Because there is no significant difference in growth rates between plots for either species after 1961, however, it can be concluded that growth rates of the northern red oak and red maple in the footprint of the eddy-flux tower appear to be representative of similar stands at the Harvard Forest over the last 40 years.

Although there is no statistical difference in growth rates since 1961 between the two plots and both plots have similar stand composition and density, tree-ring analysis reveals important differences over the 20th century. First, the Tower Plot is slightly younger and more uneven aged than the LP. Second, age structure data and differences in short-term growth rates reflect different disturbance histories. Third, differences in growth rates between species are larger in the TP than in the LP. Given that the LP is older and more even-aged than TP, weaker LP red maple may have already succumbed to competition (Oliver and Larson, 1996). The Tower Plot may still be in an earlier phase of stand development. Fourth, although the impact of the 1981 gypsy moth defoliation event is similar between the TP and LP, growth rates of LP NRO following the event do not seem to be as robust as in the TP trees. If the number of white rings is an indicator of the defoliation intensity as it is in aspen (Hogg et al., 2002a), then perhaps differences in growth rates over the last two decades between TP and LP may be related to the severity of gypsy moth defoliation. It is not clear if these differences between TP and LP will become greater in the future.

Surprisingly, precipitation does not play a major role in the growth rates of NRO or red maple at the HF. In contrast, precipitation and drought has long been recognized as an important factor of growth in eastern North America (e.g., Schumacher and Day, 1939; Cook and Jacoby, 1977; Stahle and Cleaveland, 1992; Orwig and Abrams, 1997; Cook et al., 1999). Analysis of NRO growth rates versus the Palmer Drought Severity Index, which better captures the water balance or evaporative demand on plants than precipitation (Palmer, 1965), may reveal a stronger role for drought. HF red maple growth is primarily limited by cool season temperature, which accounts for 15% of following season's growth. NRO growth is mostly limited by late, growing season temperatures. In general, these findings at HF support earlier research in the Hudson Valley in NYS (Pederson et al., 2004; Chapter 2): NRO has a weaker climatic response than many species and like several other temperate species, the radial growth of red maple is mostly limited by winter temperatures.

It is unusual to find that both species are more sensitive to temperature than drought. Only red spruce (Conkey, 1986; Cook et al., 1987) and Atlantic white-cedar (Pederson et al, 2004; Chapter 2; Hopton and Pederson, in press; Appendix A) are known to be more temperature sensitive than drought sensitive in the temperate forests of eastern North America. The Atlantic white-cedar and red spruce populations were studied in New York and New England, which brings up the possibility that there may be a unique climatic response of trees in this region compared to much of the eastern U.S. For example, Atlantic white-cedar (Hopton and Pederson, in press) and loblolly pine (Cook et al., 1998) are found to be more sensitive to temperature at a northern-range-margin than elsewhere in their distribution. Perhaps HF northern red oak and red maple are growing in a similar type of geographic setting?

Gypsy moth defoliation has a stronger impact on growth rates at annual to multi-annual time-scales than climate. This finding could be confounded by the tendency of gypsy moth defoliations events to be associated with drought (Naidoo and Lechowicz, 2001). NRO are, however, more significantly impacted by gypsy moth defoliation the year after an event than most species examined in the eastern U.S. (Muzika and Liebhold, 1999). Nonetheless, NRO recovered to significantly above the 1981 ACI value by 1988. Red maple recovered during that time, but at a much slower rate. In contrast, a decline in growth rates of sugar maple following gypsy moth defoliation was not observed (Naidoo and Lechowicz, 2001). Beyond potential species differences, other differences could contribute to these somewhat disparate findings. First, sugar maple cores that were difficult to cross-date or had many missing rings were discarded prior to growth anaylsis (Naidoo and Lechowicz, 2001). Analysis at the Harvard Forest shows that red maple trees are capable of living for several years without producing radial growth rings. The same appears to be true of sugar maple (Brendan Buckley, personal communication). It is not known if missing rings in red maple are related to defoliation, but discarding the more difficult samples removes the trees that might be more susceptible to decline following defoliation (Gansner et al., 1993). Second, it is not known if the severity of defoliation of the HF red maple is comparable to the severity of the sugar maple. Severity of defoliation likely plays an important role in the recovery of growth rates. Finally, mature sugar maple trees are typically larger than red maple (Burns and Honkala, 1990). These size differences should usually translate to differences in canopy position: dominant and co-dominant for sugar maple, co-dominant or intermediate for red maple. Differences in canopy position should translate into differences in competition, which may also account for the disparity growth recovery of these maples following gypsy moth. Ultimately, gypsy moth defoliation events produced significant reductions in growth rates of NRO and red maple at the HF.

Regional Northern Red Oak Growth and Climate Sensitivity Results

a. Regional Northern Red Oak Growth

Between 1750 and 2001 NRO growth increments and trends were highly variable across the study region (Figures 13, 14). Average regional growth rates peaked between 1975-1980 and 1998-2001. Reduced growth rates are evident in association with gypsy moth defoliation events, most notably in 1981 (Figure 14). Since the 1950's, all populations have relatively constant or increased growth rates. Goodnow Mountain, HF Lyford Plot, Prospect Mountain, Rooster Hill, Sheridan Mountain and Whispering Creek experienced declining in growth rates in the last two decades.

Between 1977 and 2001 the mean regional ACI was 28.98 kg yr^{-1} (median = 29.0; SD = 2.0). Maximum ACI in this period occurred in 1998 (33.1 kg) while the smallest increment occurred in 1991 (24.9 kg). From 1990-2001, the period of overlap between Harvard Tower eddy-flux tower and tree-ring data, the mean regional ACI was 29.40 kg yr^{-1} (median = 29.40; SD = 2.4). Other years with a regional increment greater than 30 kg were 2000 and 2001. Interestingly, 1998 and 2001 are the two warmest years on record between 1960 and 2001, respectively (GISS, 2005). Yet, the year with the lowest ACI value, 1991, is the fifth warmest between 1960 and 2001. If global temperatures play a factor in NRO growth rates in the northeast U.S., the relationship must be tempered by other factors such as the timing of drought or the onset of the growing season (phenology).

The Singer Farm population has the highest ACI from 1990-2001 with an average of 90.26 kg yr^{-1} (median = 86.21, SD = 13.88) (Table 6). The next five highest have an ACI greater than 40 kg yr^{-1}. The five westernmost populations are ranked in the top ten

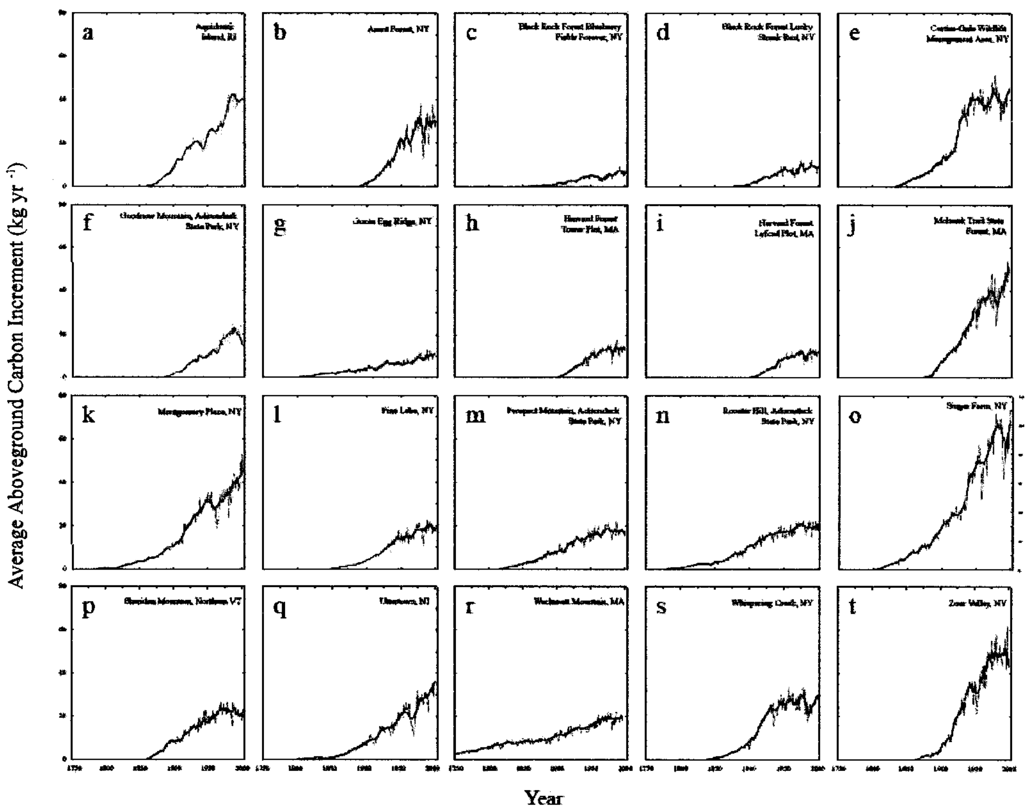

Figure 13 - Plot of Growth Rates for All Northern Red Oak Populations: a) Aquidneck Island, RI; b) Arnot Forest, NY; c) Black Rock Forest Blueberry, NY; d) Black Rock Forest Lucky, NY; e) Curtiss-Gale Wildlife Man. Area, NY; f) Goodnow Mtn., NY; g) Goose Egg Ridge, NY; h) Harvard Forest Tower Plot, MA; i) Harvard Forest Lyford Plot, MA; j) Mohawk Trail State Forest, MA; k) Montgomery Place, NY; l) Pine Lake, NY; m) Prospect Mtn, NY; n) Rooster Hill, NY; o) Singer Farm, NY; p) Sheridan Mtn., VT; q) Uttertown, NJ; r) Wachusett Mtn., MA; s) Whispering Creek, NY; and t) Zoar Valley, NY. See text for more details. A weighted curve was used on each curve to emphasize decadal-scale variations in growth rates. Note that the y-axis of the Singer Farm plot (o) has a different scale.

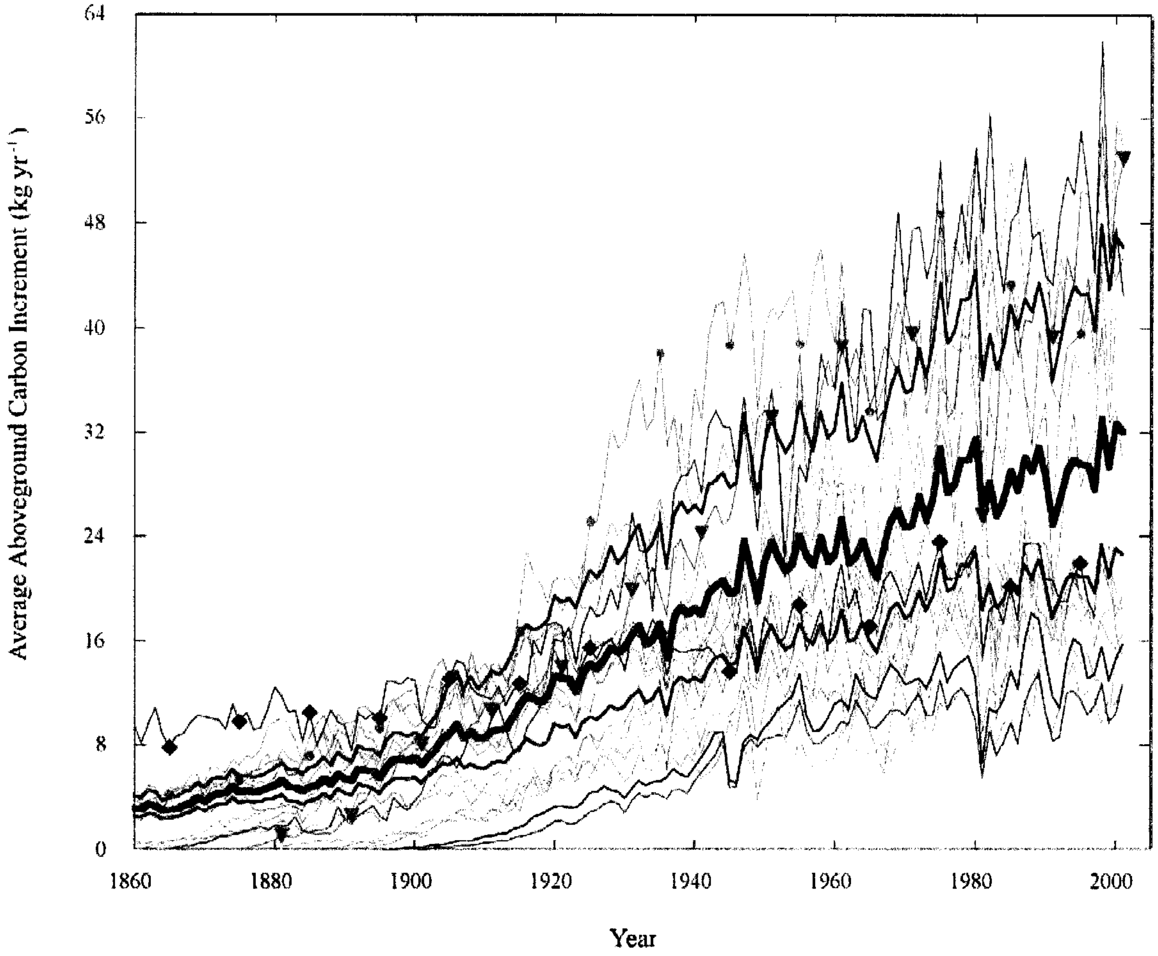

Figure 14 - Regional Northern Red Oak Growth Rates from 1860-2001. Individual ACI curves are plotted against the regional average. The highest ACI value occurred in 1998. Regional average is the thick green line. Its 95% confidence limits are the thin green lines. Confidence limits are not plotted for any other curves to preserve figure clarity. Likewise, the Singer Farm is not plotted because its growth rates are well above any other in this study. The Harvard Forest growth curves are at the bottom: red line = Tower Plot, orange line = Lyford Plot. Other populations of note are: purple line = Zoar Valley, which has the highest ACI value of 1998 except for the Singer Farm; light blue with solid inverted triangles = Mohawk Trail State Forest, which has the tallest-known NRO in the northeastern U.S.; Orange line with solid dots = Curtis-Gale Wildlife Management Area, which experienced a significant change in growth rates with the loss of the American chestnut in the early-1920s; Dark blue line with solid diamonds = Wachusett Mountain, which is an old-growth population and has the oldest-known NRO.

Table 6 - Northern red oak populations ranked by average aboveground mean carbon increment (kg yr^{-1}) from 1990-2001.

Population	**Mean**	**Median**	**Standard Deviation**	**Median Stand Age**
Singer Farm	86.21	88.94	13.88	127.0
Zoar Valley	48.70	48.20	5.67	84.5
Mohawk St. Forest	46.38	45.29	5.45	103.0
Montgomery Place	45.52	44.38	5.75	135.5
Aquidneck Island	44.28	43.73	5.62	103.5
Curtiss-Gale	40.35	39.32	4.12	149.8
Uttertown	35.71	36.05	4.45	144.5
Arnot Forest	30.38	30.56	5.32	99.5
Regional Average	***29.40***	***29.40***	***2.38***	***n/a***
Whispering Creek	28.50	27.84	2.44	111.9
Sheridan Mountain	20.66	20.28	1.53	106.0
Wachusett Mountain	19.93	19.93	1.78	205.0
Goodnow Mountain	19.78	19.17	2.80	79.5
Rooster Hill	19.30	19.35	2.01	118.5
Pine Lake	18.52	18.56	1.38	99.5
Prospect Mountain	17.15	17.40	1.09	147.5
BRF Lucky	14.84	15.03	2.34	84.5
HF - Tower Plot	**14.08**	**14.50**	**1.68**	**72.0**
Goose Egg Ridge	11.48	11.53	1.46	187.5
BRF Blueberry	11.47	12.02	1.61	120.0
HF - Lyford Plot	10.83	10.76	1.45	95.0

with three of these populations ranked in the top five. Growth rates of the HF populations are ranked towards the bottom for this time period with the HF Lyford Plot ranked last.

After 1930, the time when most trees had canopy status, annual growth rates at Singer Farm are significantly higher than all other populations except for Zoar Valley, although there is no difference between the two populations in 1960 and from 1990-1999 (not shown). There is no significant difference between Zoar Valley and the regional average (Figure 14). Growth rates of the Wachusett Mountain population are not significantly different than the regional average between 1930 and 2001 despite it being a part of an old-growth forest containing the oldest-known NRO. Black Rock Forest (BRF)

Blueberry and Goose Egg Ridge are significantly below the regional average. BRF Lucky is significantly below the regional mean except for the early-1950s, early-1970s and early-1990s.

Harvard Forest NRO have some of the lowest annual rates of carbon increment regionally (Figures 13, 14). After 1952, growth rates of the Tower Plot NRO are significantly below the regional average from 1956-1959, 1981-1984, 1992, 1996 and 1999-2000 (Figure 15). Growth rates of the Lyford Plot are below the regional average between 1930 and 2001.

Initial analyses suggested that age is not a limitation of NRO growth rates and that older populations seemed to have higher growth rates. For example, the Wachusett Mountain NRO population has significantly higher growth rates between 1990 and 2001 than the HF NRO populations (Table 6), which are among the youngest populations sampled. Therefore, an analysis was made between non-climatic factors (age structure, stand structure, tree size and geographic location) and average NRO growth rates and trends from 1977 to 2001 (Table 7; Figure 15). This period was chosen for analysis as it likely represents the longest time in which tree-ring analysis estimates of growth rates is not compromised by changes in stand structure (Dave Hollinger, personal communication). As it is well established that site quality controls productivity, each time-series of ACI was standardized to test what non-climatic factors constrain tree-level productivity in the absence of site quality. This index is termed the site standardized average aboveground carbon increment (SACI).

The strongest relation between average ACI from 1977-2001 is average population DBH and standard deviation (SD) of population DBH (Table 7). Populations

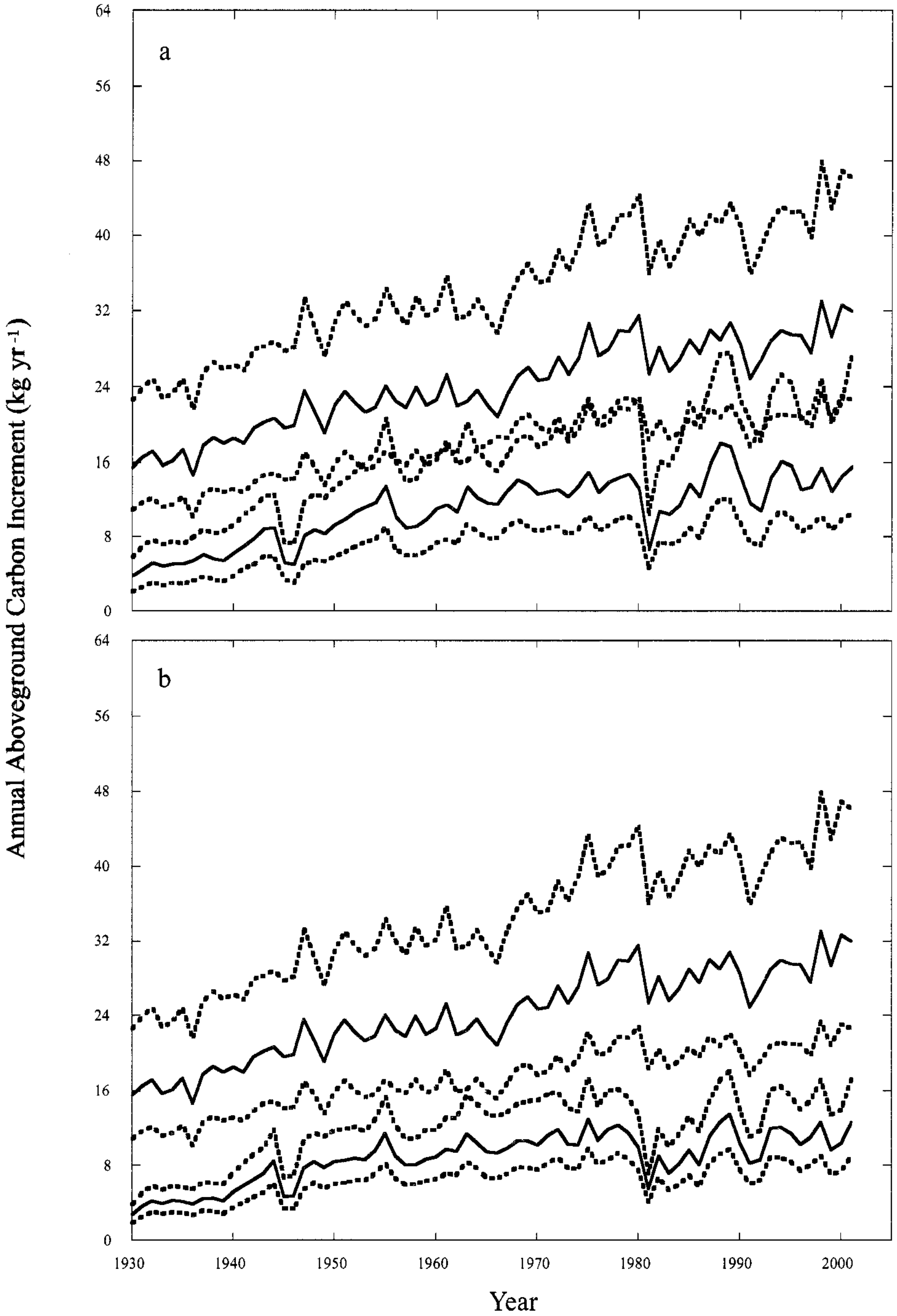

Figure 15 - Growth Rates of Harvard Forest Northern Red Oak Versus the Regional Average. ACI for the Tower Plot, red line in (a), is not significantly different than the regional average (green line) most of the time between 1950 and 2001. Lyford Plot ACI, blue line in (b), is significantly less than the regional average for the entire record. Dashed line represent 95% confidence limits.

Table 7 – Correlations between average aboveground carbon increment (ACI) of northern red oak and trends between 1977 and 2001[a] and population age structures, stand characteristics and geography. Bold numbers are significant at $p<0.05$ level: * = significant at < 0.05 level; ** = significant at < 0.01 level; *** = significant at < 0.001 level. Italic correlations are significant at $p < 0.10$ level. Correlations in light purple indicate likely autocorrelated variables and are not discussed. Population variables used are: Ave. Age = average minimum tree age at coring height (n=20 populations available for testing). Med. Age = median minimum tree age at coring height (n=20). SD Age = standard deviation of minimum tree age at coring height (n=20). Ave. ACI = 25 year average of annual aboveground carbon increment (n=20). ACI Trend = 25 year trend of annual aboveground carbon increment (n=20). SACI = 25 year average of standardized aboveground carbon increment (n=20). SACI Trend = 25 year trend of standardized aboveground carbon increment (n=20). Ave. BA = average stand basal area (n=18). SD BA = standard deviation of average stand basal area (n=15). Ave. DBH = average tree diameter at breast height (n=19). Med. DBH = median tree diameter at breast height (n=19). SD DBH = standard deviation of tree diameter at breast height (n=19). Lat. = population latitude (n=20). Long. = population longitude (n=20).

	Ave. Age	Med. Age	SD Age	Ave. ACI	ACI Trend	SACI	SACI Trend	Ave.BA	SD BA	Ave. DBH	Med. DBH	SD DBH	Lat.	Long.
Ave. Age	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Med. Age	**0.945** ***	-	-	-	-	-	-	-	-	-	-	-	-	-
Std. Dev. of Age	**0.567** **	**0.599** **	-	-	-	-	-	-	-	-	-	-	-	-
Ave. ACI	0.160	0.004	0.307	-	-	-	-	-	-	-	-	-	-	-
Trend in ACI	0.048	0.053	0.129	0.231	-	-	-	-	-	-	-	-	-	-
SACI	**0.488** *	**0.523** *	**0.640** **	*0.370*	0.146	-	-	-	-	-	-	-	-	-
SACI Trend	0.085	0.064	0.002	0.150	**0.885** ***	*0.423*	-	-	-	-	-	-	-	-
Average Basal Area	0.227	0.140	0.212	0.060	0.294	0.148	0.278	-	-	-	-		-	-
Std. Dev. of BA	0.141	0.213	0.003	0.033	0.263	0.087	0.160	0.334	-	-	-	-	-	-
Average DBH	0.173	0.273	*0.414*	**0.866** ***	0.058	*0.395*	0.059	0.317	0.046	-	-	-	-	-

	Ave. Age	Med. Age	SD Age	Ave. ACI	ACI Trend	SACI	SACI Trend	Ave.B A	SD BA	Ave. DBH	Med. DBH	SD DBH	Lat.	Long.
Median DBH	0.253	0.301	0.350	**0.761** ***	0.146	0.362	0.113	0.318	0.016	**0.977** ***	-	-	-	-
Std. Dev. of DBH	0.050	0.151	**0.542** *	**0.893** ***	0.346	**0.459** *	0.167	0.080	0.164	**0.782** ***	**0.685** ***	-	-	-
Lat.	0.038	0.056	0.031	0.103	**0.525** **	0.352	**0.654** **	*-0.401*	0.123	0.075	0.040	0.166	-	-
Long.	0.185	0.106	0.024	**0.556** **[b]	**0.452** * [c]	0.195	0.315	0.130	0.126	*0.380*	0.301	**0.476** *[d]	0.072	-

[a] = The trend for Wachusett Mountain in annual carbon increment and 25-year average is calculated for the 1973-1997 period.

[b] = Removal of the Singer Farm population, a population with big trees in the far west of study area, causes the correlation to become non-significant (r = 0.365).

[c] = Removal of the Singer Farm population, a population with big trees in the far west of study area, causes the correlation to become non-significant (r = 0.278).

[d] = Removal of the Singer Farm population, a population with big trees in the far west of study area, causes the correlation to become non-significant (r = 0.221).

with larger trees and a wider spread of tree sizes have higher growth rates. These factors are only weakly correlated versus SACI. Standardized ACI is only weakly correlated to average DBH, although it is significantly correlated to SD of population DBH.

SACI is significantly correlated to age. Populations with older trees and a higher SD of ages have higher average growth rates (Figures 16a, b). Populations with older trees also have a higher SD of ages (Table 7). SD of population ages is significantly correlated to SD of population DBH, but only weakly correlated (p level > 0.05 and <0.10) to average DBH.

There are significant correlations between longitude and average population DBH, standard deviation of population DBH and average ACI. These correlations suggest that average ACI and tree size increases moving west (Table 7). The large NRO in the western end of the study region at the Singer Farm compromises these correlations. Removal of the Singer Farm population makes this relation non-significant (Figure 16c).

The strongest influence on the trend in growth rates between 1977 and 2001 is latitude, especially versus SACI (Table 7; Figure 16d). The trend in annual growth rates decreases as latitude increases. There is also a significant relation between longitude and trend in growth rates. Again, once Singer Farm is removed from the analysis, the significant correlation is lost. There is no significant relation between longitude and trend in growth rates, however, if site quality is standardized. These results indicate that if there is a longitudinal trend in growth rates, it is related to site productivity. Perhaps the most intriguing finding of this analysis is that there is no relation between age and trend of NRO growth rates (Table 7; Figures 16e, f).

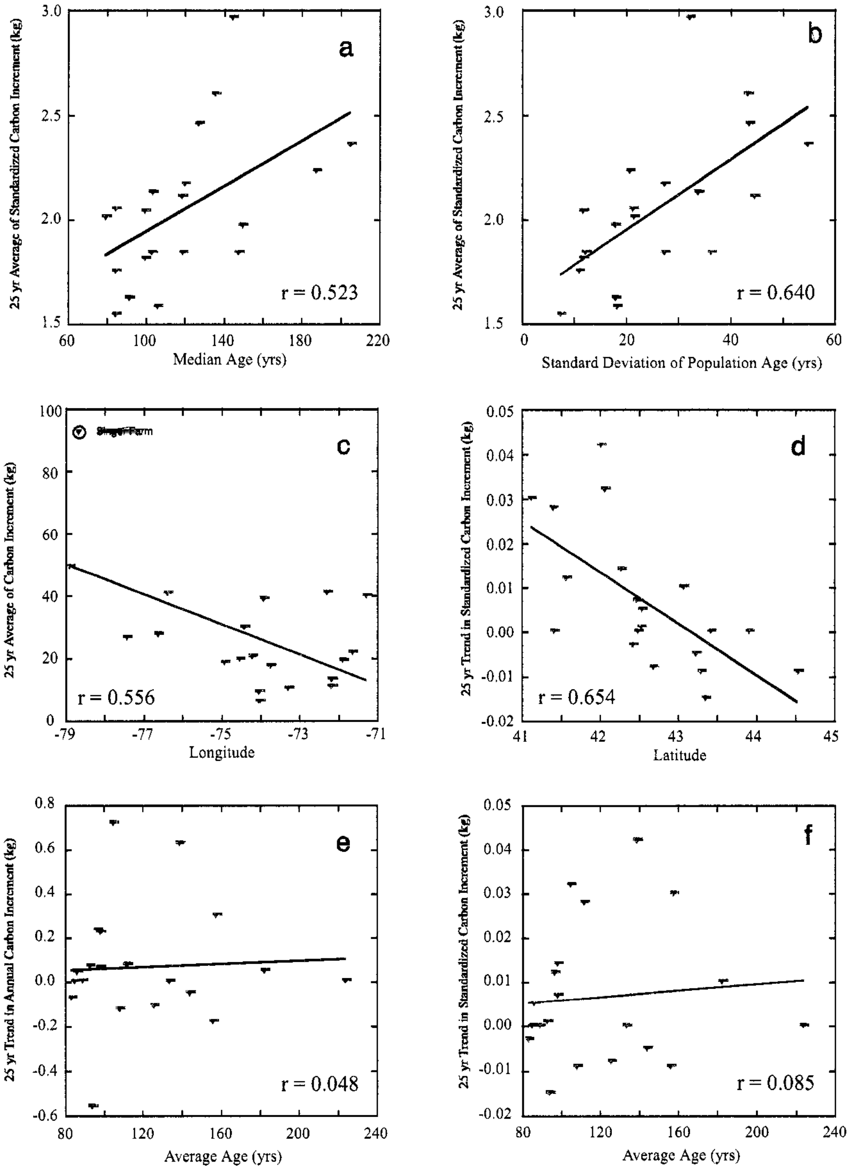

Figure 16 - Non-Climatic Factors Versus Northern Red Oak Growth Rates. a) Median age vs. 25-yr average of standardized ACI, b) standard deviation of population age vs. 25-yr average of standardized ACI, c) longitude vs. 25-yr average of ACI, d) latitude vs. 25-yr average of standardized ACI, e) average age vs. 25-yr trend of ACI and f) average age vs. 25-yr trend of standardized ACI. Note in graph (c): removal of the Singer Farm population results in a non-significant correlation between longitude and ACI. See text for further discussion.

b. Correlation Between Annual NRO Growth and Climate

Tables 6-8 shows the significant relations between NRO growth and precipitation (PCP), average minimum monthly temperature (T_{min}) and average maximum monthly temperature (T_{max}), respectively. Populations are presented longitudinally from west to east because patterns emerged in this arrangement. Arrangement of populations alphabetically and latitudinally did not reveal any similar observable patterns.

The most common climatic factor influencing NRO growth in the northeastern U.S. is June and July precipitation (Table 8). June precipitation is more strongly and consistently related to growth than July precipitation. Conspicuously, growth of the Massachusetts and the Singer Farm populations are not significantly limited by growing season drought. Growth of five populations is significantly and positively correlated with prior December and current January precipitation. The most unusual, but consistent relation between NRO growth and precipitation is a strong negative correlation with February precipitation. Populations with this correlation are found east of the Catskill Mountains in NYS and south of Mohawk Trail State Forest, MA.

Correlation between NRO growth and T_{min} are less consistent and generally weaker than the correlations with precipitation (Table 9). The most consistent and significant relations are inverse correlations with March, April and June temperatures, with June temperatures being the strongest and most consistent. Positive correlations to late-growing season T_{min} were calculated at northern-range-margin and mountainous locations.

NRO growth has a slightly different relation to T_{max} than it does to T_{min} (Table 10). Nine populations have weak, but positive correlations between growth and prior winter temperatures. Two interesting patterns are found in the relation of NRO growth and T_{max}. First, there is a clustering of positive correlations to July and August maximum

Table 8 - Correlation between precipitation and annual radial increment of the residual chronologies of northern red oak populations from western N.Y. State and central New England. Sites are arranged by longitude.

	pM	pA	pM	pJ	pJ	pA	pS	pO	pN	pD	J	F	M	A	M	J	J	A	S
Zoar																**0.296** *	_0.208_		
Sing						_0.222_					_-0.215_								
WC									**-0.312** *			_0.209_							
Arnot							_0.239_				**0.331** **				**0.269** *	**0.396** **			
Curt		_0.187_	**0.254** *			_0.176_										**0.293** *	**0.213** *		
Pine							_0.233_				_0.222_					**0.428** ***	**0.248** *		
Roost						**0.311** *										**0.354** **	**0.272** *		
Utter											**0.312** **					**0.255** *	**0.297** *		
Good															**0.336** **	**0.444** ***	**0.262** *		
BR L						_0.236_	_0.220_					**-0.318** **	**0.242** *				_0.226_		
BR B					_0.234_		_0.211_					**-0.379** **	_0.241_			**0.256** *	_0.241_		
M_Pl												_-0.221_			_0.203_	**0.397** *			
Pro	**-0.257** *															**0.345** **	_0.218_		
Goose					_0.201_				_0.205_							**0.355** **			
MTSF								_-0.214_		**0.321** **		**-0.260** *							
HF L		**-0.257** *	_-0.229_	**-0.260** *								**-0.263** *						_0.221_	
HF T												**-0.289** *	**0.274** *					_0.208_	
Wachu									**-0.340** **	**0.261** *		**-0.273** *							**0.256** *
Sherid	_0.230_			**-0.286** *	_-0.235_								**-0.269** *			**0.326** **	_0.218_	_-0.239_	
Aquid									_-0.217_			_-0.220_				**0.286** *	_0.232_		

Table 9 - Correlation between average monthly minimum temperature and annual radial increment of the residual chronologies of northern red oak populations from western N.Y. State and central New England. Sites are arranged by longitude.

	p M	pA	pM	PJ	pJ	pA	pS	pO	pN	pD	J	F	M	A	M	J	J	A	S
Zoar																**-0.268** *			
Sing										**0.364** **			*-0.230*	**-0.285** *					
WC														**-0.418** *		*-0.211*			
Arnot																			
Curt		*-0.237*														**-0.225**			
Pine							*0.207*										**0.309** *	*0.234*	*0.206*
Roost													**-0.269** *						
Utter					*-0.203*						*0.222*						*0.228*		
Good																	**0.328** **	**0.290** *	
BR L							*-0.234*									**-0.289** *			
BR B							**-0.261** *									**-0.245** *			
M_Pl																	**0.305** *		
Pro								*0.236*											
Goose										**0.221** *				**-0.298** *					
MTSF					**-0.338** **													**0.281** *	
HF L		**-0.244** *	*-0.213*										**-0.281** *	*-0.236*					
HF T		*-0.200*				**-0.253** *													
Wachu					*-0.220*		*-0.210*		*-0.212*				*-0.222*			*-0.229*			
Sherid					**-0.279** *	*-0.220*											**0.325** **		
Aquid				**-0.307** *												**-0.373** *			

Table 10 - Correlation between average monthly maximum temperature and annual radial increment of the residual chronologies of northern red oak populations from western N.Y. State and central New England. Sites are arranged by longitude.

	p M	p A	pM	pJ	pJ	pA	pS	pO	pN	pD	J	F	M	A	M	J	J	A	S
Zoar																**-0.496** ***	*-0.207*		
Sing										**0.358** **				**-0.282** *		-0.321 **			
WC														**-0.263** *		**-0.320** **			
Arnot															**-0.290** *	**-0.377** **	**-0.286** *		
Curt																**-0.273** *			
Pine																**-0.314** *			
Roost													**-0.304** *						
Utter											*0.235*					**-0.291** *			
Good															**-0.296** *		*-0.238*		
BR L						**-0.265** *	**-0.301** *	*0.236*			*0.234*					**-0.389** **	*-0.225*		
BR B						**-0.245** *	**-0.312** *				**0.249** *					**-0.362** **			
M_Pl					*0.209*						*0.211*								
Pro			**-0.246** *													**-0.257** *			
Goose										**0.227** *				**-0.259** *		*-0.199*			
MTSF									*0.229*		**0.309** *						**0.266** *	**0.269** *	
HF L			*-0.220*			*-0.226*											**0.400** ***		
HF T					*-0.204*	**-0.259** *				*0.215*							**0.386** **		
Wachu												*-0.238*				*-0.221*			
Sherid						**-0.276** *												**0.218**	
Aquid				*-0.240*						*0.220*						**-0.342** **			

temperatures in central Massachusetts and northern Vermont. The second is the absence of relation to prior growing season temperatures in the western end of the study region.

c. Gypsy moth defoliation events and NRO growth

Gypsy moth events were identified by the presence of unusually narrow latewood widths and confirmed with gypsy moth outbreak maps (USFS, 2003) or eyewitness accounts (*i.e.,* Bruce Gilman for the Whispering Creek population). Tree-ring records show that gypsy moth defoliation events had the strongest impact on multi-annual NRO growth over the last century. Among surviving NRO trees, these events caused an average reduction in growth of 36.7% versus the prior five years of growth (Table 11). Growth rates recovered to within 10% of the prior 5-year average within five years after the gypsy moth event. In comparison, the 1960s drought caused growth rates at Montgomery Place, NY to decline only 8.5% versus the prior 5 years. Five years after the 1960s drought, growth rates were 32.0% greater than the five years prior to the drought. Montgomery Place was the only population with a considerable reduction in growth similar to what has been found previously in other species (Cook and Jacoby, 1977; Cook, 1991). Further, while dramatic one-year declines in growth rates in non-gypsy moth areas (Adirondack Mountain region – Rick Fenton, NYS forester, personal communication; Sheridan Mountain – Steve Slayton, Caledonia County state forester, personal communication) declined by 34.2%, they recovered to near pre-disturbance rates within 5 years. Gypsy moth defoliation and its impacts on growth rates are discussed in greater depth in Appendix B.

Table 11. Changes in growth rates 5-years prior and post to a large disturbance event. Growth rates are determined through the averaging of above ground carbon increment (ACI). Numbers in parentheses in the average of population events section represent standard deviation of percent change in growth.

Event Type (Year(s))	Ave. ACI 5-yrs Prior (SD)	Event ACI as a % of Prior 5-yrs	Ave. ACI 5 yrs Post to Event (SD)	% Post Event ACI vs. Prior ACI
Gypsy Moth				
Arnot Forest (1983)	30.37 (6.8)	40.7	20.32 (4.9)	66.9
BRF Blueberry Fields (1981)	5.50 (0.3)	58.9	4.98 (0.4)	90.5
BRF Lucky Streak (1981)	10.55 (1.2)	54.3	7.84 (0.5)	74.3
Goose Egg (1981)	10.46 (0.7)	81.3	8.45 (0.8)	80.8
HF Tower Plot (1945-46)	8.30 (1.2)	65.8	9.48 (0.9)	114.2
HF Tower Plot (1981)	13.72 (0.8)	46.4	11.70 (1.0)	85.3
HF Lyford Plot (1945-46)	6.95 (1.3)	69.2	8.43 (0.2)	121.3
HF Tower Plot (1981)	11.68 (1.1)	47.9	8.65 (1.1)	74.0
Mohawk Trail State For. (1981)	37.42 (5.9)	65.2	34.91 (3.0)	93.3
Montgomery Place (1981)	34.81 (0.8)	67.3	34.77 (1.6)	99.9
Pine Lake (1983)	18.70 (2.2)	54.2	16.90 (1.1)	90.4
Prospect Mountain (1981)	17.66 (1.0)	75.0	17.08 (1.2)	96.7
Wachusett Mtn. – 1945-46	14.35 (0.3)	87.9	15.57 (1.3)	108.5
Wachusett Mtn. (1981)	20.26 (1.2)	67.4	16.81 (2.0)	83.0
Whispering Creek (1983-86)	32.03 (2.0)	68.7	22.57 (2.7)	70.5
Average (n=15)	-	63.3 (13.1)	-	90.0 (16.1)
1945 (n= 3)	-	74.3 (11.9)	-	114.7 (6.4)
1981 (n=12)	-	60.6 (12.3)	-	83.8 (10.7)
Drought				
Montgomery Place (1964-66)	24.46 (1.8)	91.5	32.3 (1.0)	132.0

Event Type (Year(s))	**Ave. ACI 5-yrs Prior (SD)**	**Event ACI as a % of Prior 5-yrs**	**Ave. ACI 5 yrs Post to Event (SD)**	**% Post Event ACI vs. Prior ACI**
Unknown				
Mohawk Trail St. For. (1953)	30.86 (6.1)	72.6	32.08 (1.6)	104
Singer Farm (1990-1991)	100.76 (10.8)	65.0	82.23 (8.6)	81.6
Uttertown (1969-1971)	18.57 (4.2)	67.7	25.25 (5.8)	136.0
Unknown in Non-Gypsy Moth Areas				
Goodnow Mtn. (1949)	9.72 (1.7)	35.8	9.76 (2.3)	100.4
Goodnow Mtn. (1983)	19.32 (1.7)	79.6	21.37 (2.4)	110.6
Rooster Hill (1983)	20.78 (1.2)	73.0	18.57 (1.8)	89.4
Rooster Hill (1992)	20.81 (1.4)	68.9	19.13 (1.5)	91.9
Sheridan Mtn. (1986)	22.0 (1.3)	71.8	23.57 (2.2)	107.1
Non-Gypsy Moth Area Ave. (n=5)	-	65.8 (17.2)	-	99.9 (9.2)
All Drought & Unknown Ave. (n=9)	-	69.5 (14.9)	-	105.9 (18.4)
Ave (minus Singer Farm & Uttertown)	-	70.5 (17.00)	-	105.1 (15.2)
Ave (minus Singer Farm, Uttertown & Rooster Hill)	-	70.3 (20.8)	-	110.8 (12.4)

d. Regional Site Productivity Indices (RACI)

The realigned average aboveground carbon increment curves shows that all populations have increased growth rates over the first 70 years except for the HF Lyford Plot (Figure 17). RACI curves cluster into three main groups: six populations above the

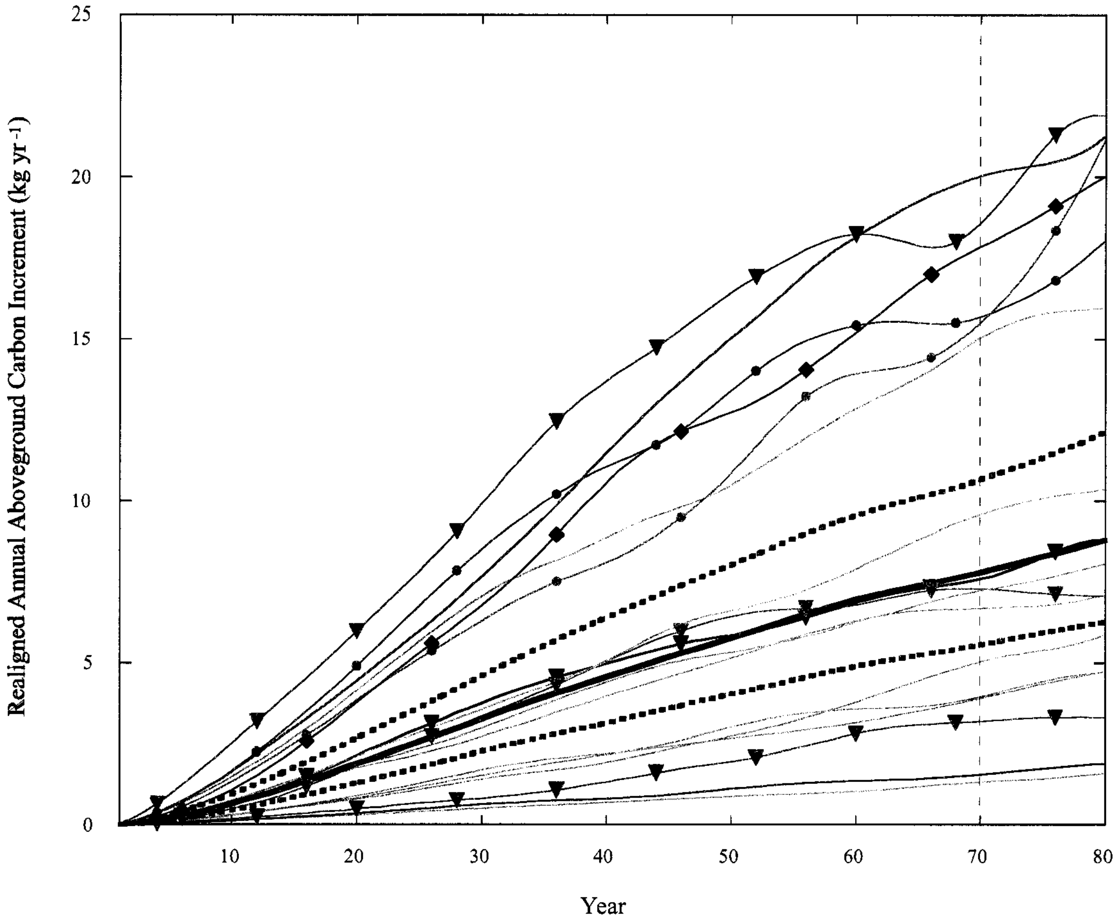

Figure 17 - Regional Re-aligned Average Aboveground Carbon Increment (RACI). Analysis is performed on the first 70 years (dashed light gray vertical line), after which tree replication for some populations limit interpretation. The regional average is the solid green curve. Dashed green lines represent the 95% confidence limits for the regional average. Confidence limits for other curves are not shown to aid figure clarity. Both Harvard Forest populations fall directly on the regional average (red line with solid inverted triangles = Tower Plot; light blue line with solid inverted triangles = Lyford Plot). Other plots of note: brown line = Mohawk Trail State Forest, MA, which has the highest RACI at 70 years and has the tallest-known NRO in the northeastern U.S.; dark orange line with solid inverted triangles = Singer Farm, which has the highest average population DBH in this study; purple line with solid triangles = Zoar Valley, which may be the tallest hardwood forest in the northeastern U.S.; pink line with solid circles = Aquidneck, RI; light orange line with solid circles = Curtiss-Gale; uppermost gray line = Arnot Forest; dark pink line with solid inverted triangles = Black Rock Forest Blueberry, which is a low-productivity, permanent repeated measures plot; dark blue line = Wachusett Mountain, which is a classic old-growth forest and has the oldest-known NRO; and lowest gray line = Goose Egg Ridge, which is composed of primarily of trees from an old-growth forest. Pine Lake and Warren-Cutler, within the CL of the regional mean, and Black Rock Forest Lucky, below the lower 95% CL of the regional mean, curves are not shown to aid figure clarity.

upper 95% confidence limit (CL) of the regional mean, seven populations within the 95% confidence limits of the regional mean (Pine Lake and Whispering Creek curves not shown to aid figure clarity) and a group of seven below the lower 95% CL of the regional mean (BRF Lucky curve not shown to aid figure clarity). All populations in the middle group are not significantly different than the regional mean. Potential site productivity at the Harvard Forest is virtually identical to the regional mean.

Over the entire 70-year period, only the Singer Farm population RACI is significantly above the regional mean (not shown – see caption for Figure 17). Arnot Forest, which has the lowest RACI curve at year 70 of populations in the upper group, is significantly above the regional mean after year 35, as is Zoar Valley. Aquidneck Island, RI is significantly above the regional mean between year 10 and 60. Curtiss-Gale is significantly above the regional mean after 50 years.

Of the lowest group of RACI curves, Wachusett Mountain and Goose Egg Ridge are significantly below the regional mean for the entire period. BRF Blueberry is significantly below the regional mean until year 62. RACI curves for all other populations of the lower group are not significantly different than the regional mean.

Regional Northern Red Oak Growth Discussion:

Regional growth rates have increased since the 1950s and peaked from the late-1970s and late-1990s to early-2001. As growth of NRO is most responsive to early-growing season drought and less responsive, but positively correlated to winter temperatures, climate may be playing a role in the increased growth rates. Drought has become less frequent since the 1950s in the northeast U.S. (NRCC, 2003). Occurrence of moderate, severe, or extreme drought was the lowest in the northeastern U.S. in the 1970s and extreme droughts were infrequent between the late-1990 and 2001 (NERC, 2003). Winter temperatures have increased nearly three-times faster than annual temperatures in the study region since 1895 (Keim and Rock, 2002). Also, there were no comparable defoliation events like 1981 between 1975 and 1980 and only a few small and scattered gypsy moth defoliation events between 1993 and 2002 (USFS, 2003). Peaks in NRO growth rates coincide with periods of no or small defoliation events, less frequent and less severe drought events and increased winter temperatures. The trend in growth rates coincides with positive trends in the dominant climatic factors limiting NRO.

Harvard Forest northern red oaks were among the least productive populations over the 20th century. Part of the reason for this appears to be related to the trees being among the youngest populations sampled. Therefore, sites dominated by northern red oak, especially those with older trees, could be sequestering significantly more atmospheric CO_2 than the forest surrounding the Harvard forest eddy-flux tower if tree-growth rates are somewhat representative of stand-level productivity. Research on a chronosequence of Norway spruce shows that tree growth increased more than stand level productivity (Mund et al., 2002), which suggests that the increasing growth rates of older NRO might not be representative of an equal increase in stand-level productivity. Nonetheless, the spruce study does suggest that increasing stand level productivity may be partially related to increased tree growth rates.

RACI does show that the site upon which the Harvard Forest NRO grows may be typical for the northeastern U.S. NRO forests sampled for this study. The HF populations fall squarely on the regional average RACI. In this sense the Harvard Forest can be considered a typical mid-latitude northern red oak site (Goulden et al., 1996) due to its site qualities. Thus, it can serve as a model of carbon sequestration for NRO-dominated forests of a similar age in the northeastern U.S.

Of the non-climatic factors available for study, the best predictor of average ACI from 1977-2001 is average tree DBH and standard deviation of DBH. These results may not appear to be too surprising as they are consistent with earlier studies indicating that growth rates are positively correlated to site productivity and tree size (Ryan et al., 1997; Schuler, 2004; Wyckoff and Clark, 2005; Chapter 4). Further, the results might appear circular in that reconstructed inner-bark DBH is used to estimate growth rates from allometric equations. Allometric equations predict larger aboveground biomass with larger trees. These equations, however, do not predict how annual growth rates should change as tree size increases. In fact, one hypothesis on the relation between tree size and growth rates predicts that growth rates decline as trees become larger (Weiner and Thomas, 2001). Evidence here showing a positive relation between tree size and growth rates contradicts this hypothesis. NRO in this study include populations with some of the largest-known individuals in terms of diameter and tree height in the northeastern U.S. It would be instructive, however, to continue this line of NRO of research into the southeastern U.S. where tree sizes are generally greater so that a wider range of tree sizes could be tested. Regardless, results here show that NRO annual growth increment is positively correlated to tree size.

Once differences in site quality are removed, average, median and standard deviation of population tree age is the best-correlated non-climatic factor of NRO ACI in the sampled stands across New York State and New England from 1977-2001. These findings support a study of white oak, chestnut oak and yellow-poplar along the Appalachian Mountains and from Alabama to Michigan showing increasing growth rates in older trees (Chapter 4). Temperate forests show the greatest age-related increase in stand-level productivity globally (Pregitzer and Euskirchen, 2004). Combined, these findings add more weight to the emerging pattern that age is not the most limiting factor of tree growth rates (Marshall, 1927; Assman, 1970; Lamarche et al., 1984; Carey et al, 2001; Latham and Tappeiner, 2002; Knohl et al., 2003).

The interrelationships between standardized ACI, SD of population age and tree diameter suggest that old forests can be relatively productive. Regionally, higher SD of tree ages, which is strongly correlated to average and median tree age, is significantly correlated to higher tree-level productivity. Older NRO populations also tended to have larger tree diameters and a higher SD of tree DBH. Forests develop a great range of tree diameters and ages as they approach an old-growth condition via disturbance (Oliver and Larson, 1996). Evidence presented here leads to a hypothesis that disturbance is important for tree productivity at the stand and forest level. A comparison of the Harvard Forest populations provides a specific example. The Lyford Plot was chosen for comparison to the Tower Plot because of similar static stand characteristics. Tree-ring analysis has shown that the LP is more even-aged than the TP and tree-level productivity of NRO and red maple is less than TP, though not significantly less productive. The relation between SD of NRO age and diameter and tree-level productivity found here is reminiscent of the hypothesis that increased biodiversity increases ecosystem productivity. In this case, the increased diversity of tree age and diameter may be accessing more of the energy niches available in the ecosystem.

Another provocative finding is that trends in growth rates are correlated to latitude, not age. As age is not correlated to latitude, it seems that it is solely latitude influencing the trend in growth rates. Latitude must be a proxy for other factors as an influence of trends in growth rates. One possible factor is that New England climate has gotten warmer and wetter in the south than in the north (Baron and Smith, 1996; Hodgkins et al., 2002; Keim and Rock, 2002). New York State has been less well studied, especially at a high spatial resolution. An overview of the few analyses in NYS, however, would suggest similar climatic change trends in New York (Keim and Rock, 2002; Stager and Martin, 2002). These results indicate that environmental factors, such as patterns of geographic climate change, may constrain trends in NRO growth rates.

Measurements at the Harvard Forest since 1990 indicate that 10% was added to standing biomass, while atmospheric deposition has added over 64 kg N ha^{-1}, and average CO_2 concentrations have increased by over 10 ppm. Such consistent uptake suggests that decadal-scale uptake is driven by intrinsic ecosystem properties like NRO succession and land-use (Barford et al., 2001). A recent study of eastern U.S. forest inventory data supports the land-use/age structure hypothesis by concluding that carbon sequestration over the past century was the result of agricultural land afforestation and the young age of the forests (Caspersen et al., 2000). Other studies suggest that fertilization by nitrogen deposition and enhanced growth due to increasing CO_2 could be stimulating CO_2 uptake (e.g., Friedlingstein et al, 1995; Kicklighter et al., 1999; Houghton, 2002). Results here suggest that stand development is an important factor of increased NRO growth rates. The results, however, do not suggest that forest age will limit carbon sequestration. Research suggests increased carbon sequestration in old forests (*e.g.* Mund et al., 2002;

Bascietto et al., 2003). Further, changes in environmental factors and warming have been shown to increase site productivity (*e.g.* Boyer, 2001; Nigh et al., 2004). Therefore, carbon sequestration in the northeastern U.S. might not dramatically slow as NRO forests continue to develop. Favorable changes in climate and increased nitrogen deposition and atmospheric CO_2 could offset potential stand-level limitation in standing biomass and productivity.

Is RACI a Valid Index of Site Productivity?

Unfortunately, it is not yet a simple yes or no as to whether RACI reflects potential site productivity. Initial results are promising based on several lines of evidence. First, two of the three highest ranked populations, Mohawk Trail State Forest (MTSF) and Zoar Valley, are from forests with the tallest NRO or hardwood trees in the northeastern U.S. (Table 12). The Mohawk Trail State Forest population is the tallest NRO measured to date in the northeast (Bob Leverett, personal communication). Zoar Valley has the highest average height for a multi-species site index in the northeast U.S. (ENTS, 2005a, b).

Conversely, Goose Egg Ridge and Wachusett Mountain are ranked last according to RACI. Wachusett Mountain fits the classic definition of eastern old-growth forests - there is little to no evidence of logging or significant human-induced disturbance (Orwig et al., 2001). Seventy-five percent of the trees at Goose Egg Ridge come from a newly discovered old-growth forest. Chestnut oaks up to 350 years old (Pederson et al., 2004; Chapter 2) and white oaks 200-300 years old (N. Pederson, unpublished data) grow on a steep and relatively inaccessible ridge with little sign of human disturbance. Stahle and

Chaney (1994) showed that old-growth forests are typically found on unproductive sites. The fact that two old-growth forests are ranked at the bottom of an index of potential site productivity and some of the tallest forests are ranked near at the top suggests that RACI may be useful. Further comparison of RACI to site indices and measurements of stand biomass will help determine the utility of RACI.

Table 12. Ranking of NRO sites by highest RACI from post-disturbance cambial year 51-70.

Population	Mean	Median	Std Deviation
Mohawk Trail St. Forest	18.07	18.29	1.49
Singer Farm	17.84	17.97	0.48
Zoar Valley	15.38	15.36	1.63
Aquidneck	15.14	15.45	0.57
Curtiss-Gale	13.70	13.98	1.12
Arnot Forest	12.91	12.95	1.31
Montgomery Place	8.05	7.99	0.96
Whispering Creek	7.24	7.36	0.53
Regional Average	***6.92***	***6.99***	***0.59***
HF Lyford Lyford Plot	6.90	6.82	0.28
HF Tower Plot	**6.82**	**6.90**	**0.55**
Sheridan Mountain	6.30	6.32	0.61
Goodnow Mountain	6.18	6.31	0.46
Pine Lake	5.53	5.61	0.52
BRF Lucky	4.12	4.34	0.38
Uttertown	3.88	3.85	0.72
Prospect Mountain	3.55	3.57	0.21
Roost Hill	3.23	3.19	0.37
BRF Blueberry	2.73	2.85	0.40
Wachusett Mountain	1.36	1.37	0.11
Goose Egg Ridge	1.08	1.04	0.13

There is conflicting evidence as to whether the western end of the study region is more productive and thus, capable of sequestering more atmospheric CO_2. RACI indicates that sites in western New York State (WNY) have highest level of site productivity with all five WNY sites in the top eight. The lowest ranked WNY population, Whispering Creek (ranked #8), is the closest to an old-growth condition (Bruce Gilman and N. Pederson, unpublished data). Analysis between non-climatic factors and NRO growth rates suggested that a relationship of higher productivity moving from east to west is true. This relationship became non-significant with the removal of the Singer Farm. Given the EOL's and the Alleghany Plateau's lake-modified climate and bedrock geology, there is some reason to think, however, that it could be a region with higher potential productivity than the eastern end of the study region. Anecdotal evidence exists supporting this hypothesis: completion of the Erie Canal in 1825 decimated the New England farming industry. More productive soils in the Great Plains and the rising costs of farming in the eastern U.S., however, did not substantially diminish the health of the agricultural industry in the EOL and the Alleghany Plateau until the latter half of the 20th century. It could also be that there was a tendency to choose high quality sites in the western end of the NRO study region. Analysis of U.S. Forest Service Inventory and Analysis data may help sort out the conflicting evidence in this chapter. Much of the evidence presented here would suggest that the western end of the study region is more productive.

Evidence presented here suggests that RACI may be a good tree-ring based proxy of site index. Indices based on reduction of canopy competition and the 'smearing' of averaging of climate within a population holds the potential to reveal site level productivity. The best way to determine this would be to compare ranks of traditional site indices (tree heights) and measured aboveground biomass to RACI chronologies. Given the difficulty in accurately measuring tree heights, precisely dated chronologies of ring widths measured to the nearest 0.001 mm might turn out to be a good supplement to traditional site indices.

Conclusion:

Data from this study indicates that NRO at the Harvard Forest may be undergoing succession and outcompeting red maple. Growth rates of northern red oak at the Harvard Forest are among the lowest of 20 populations across the northeastern U.S. As the HF populations are among the youngest and smallest trees sampled, their rankings reflect the findings that tree size and age are positively correlated to growth rates. If individual-tree growth rates are representative of stand-level growth rates, it suggests that carbon uptake rates in the region based on rates at the Harvard Forest may be conservative.

It is difficult to predict how growth rates will change in the future. If early summer precipitation increases and winter temperatures continue to warm, NRO growth rates in the northeastern U.S. would be expected to increase. Increased June maximum temperatures, however, could exacerbate drought stress and counteract predicted winter and late-summer warming.

Even though gypsy moth defoliation events have the most significant impact on annual to multi-annual growth rates for northern red oak, ecosystems may be adapting to these events (Campbell and Sloan, 1977; Swain, 1983; Muzika and Liehbold, 1999). For example, evidence from the Pocono Mountains of Pennsylvania shows that the presence of gypsy moth over a 20-year period did not diminish growth rates of most oak species (Gansner et al., et al., 1993). Thus, future growth rates might not be as severely impacted by defoliation as in the past barring interactions with significant negative climatic events.

Age does not seem to be a primary limitation of individual-tree growth rates. Future changes in individual-tree growth rates would most likely be related to environmental factors such as a poor climatic environment for NRO growth or the influence of new invasive species. As this study has shown, the fate of individual-tree growth rates and potential carbon uptake are not tied to one factor.

Among the several aspects of this research that should be pursued, one stands out: the tree-ring based site index or RACI. Initial results suggest that the index may represent potential site productivity. Before this index is used further, however, a rigorous comparison between traditional site indices and the new method should be undertaken. Traditional site indices are based on tree heights. The difficulty of accurately measuring trees height is fairly well known. The capability of tree-ring analysis in producing highly accurate measures of growth could serve to improve quantification of site productivity and expected trends in individual-tree growth rates.

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Chapter 4: Evidence of Accelerated Growth in Old Trees

Abstract:

Radial growth analysis of 981 mix-aged trees from 46 independent stands in the eastern United States reveals a trend of increasing ring widths over the last 150 years, even for the oldest age classes and oldest-known individuals. Contrary to long-held assumptions, these results indicate that individual tree growth rate is not limited by age. Sustained rates of carbon uptake are evident when these time-series are converted to mean annual increment of aboveground carbon. These results suggest that old trees and forests can remain a vital element of the terrestrial carbon cycle.

Introduction:

A common assumption of most ecophysiological, ecosystem and carbon sequestration models informing policy decisions, such as the Kyoto Protocol, is that growth rates decline as trees age (Watson et al., 2000). This notion of overmaturity became rooted across disciplines following Odum's (1969) review of ecosystem development. Odum's forest development model was derived from three time-series of leaf biomass production that were only 20 to 80 years in length (Kira and Shidei, 1967), which is short compared to the longevity of most canopy-dominant tree species. The concept of an age-related decline in forest productivity has become an important component of management plans, expectations of carbon sequestration and ecophysiological research despite evidence suggesting that age may not limit growth rates or carbon uptake (Marshall, 1927; Lamarche et al., 1984; Carey et al., 2001; Knohl et al., 2003). Evidence indicating that age does not limit tree growth rates would support the idea that old-growth forests can have an important effect on the global carbon cycle (Schulze et al., 2000).

We examine the long-term growth rates of 981 trees of three species, white oak (*Quercus alba*), chestnut oak (*Q. prinus*) and yellow-poplar (*Liriodendron tulipifera*), growing in natural broadleaf deciduous forests of the eastern United States. Our dataset includes more than 160 trees older than 300 years and the oldest-known individuals for each species (white oak - 464 years, chestnut oak - 427 years, and yellow-poplar - 336 years). The dataset allows us to examine growth rates of trees up to their maximum known age (MKA). Given that radial growth rings in trees typically decline due to geometric constraints related to stem expansion (Cook and Kairiukstis, 1990), we do not expect ring widths and growth rates to increase as trees age. An alternative hypothesis to the age-related decline hypothesis is that growth rates increase and then decline as tree size increases (Weiner and Thomas, 2001). We test the size-related decline hypothesis on a subset of our data.

Methods:

Our data network covers nearly 400,000 km^2 and is composed of 837 oak and 144 yellow-poplar trees cored primarily in the late-1970s to early-1980s and late-1990s to 2003 (Figure 1, Tables 1, 2). Trees were primarily sampled in old-growth forests and, to a lesser extent, old, previously cut forests. Most prior studies of age-related decline in forest productivity were conducted outside of our study region and are based on coniferous species, short-lived, early successional hardwood species or even-aged forests

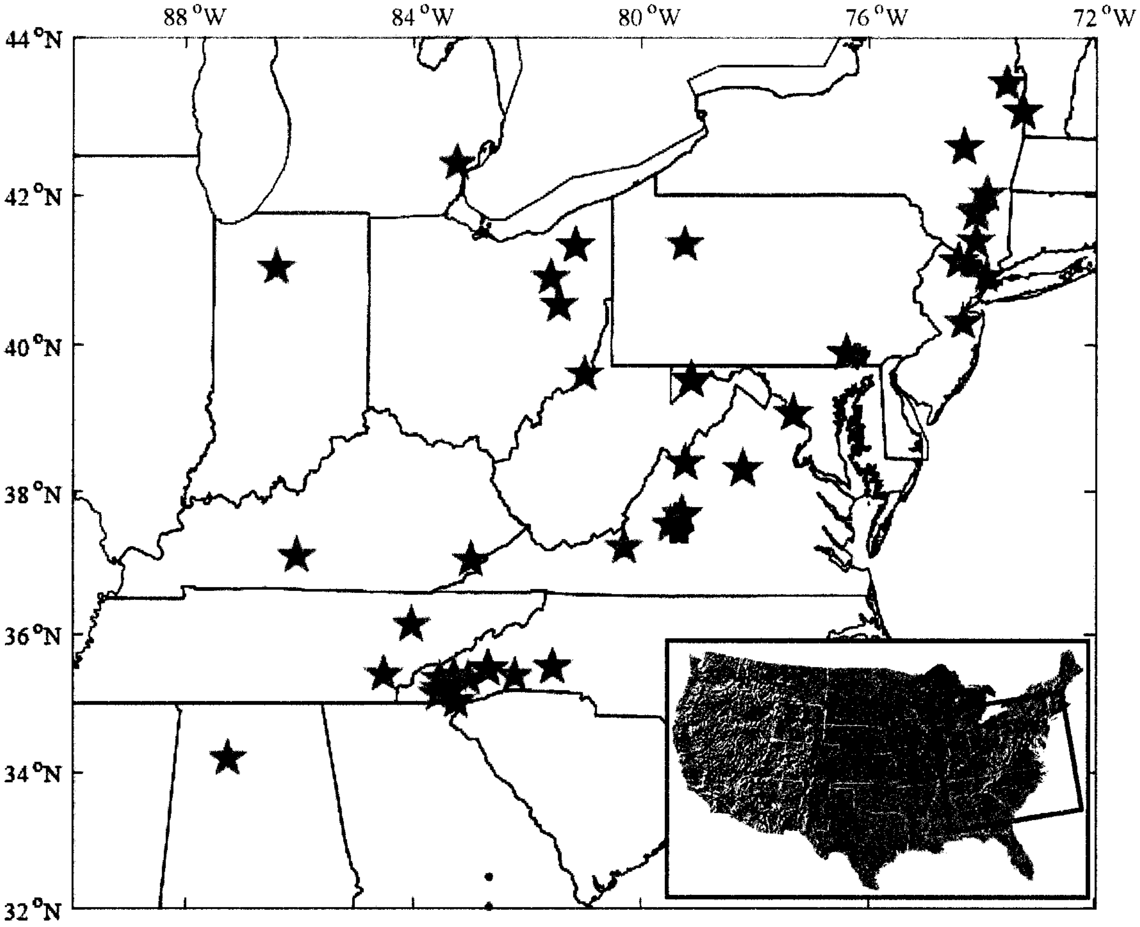

Figure 1 - Site locations of the populations sampled. Stars represent: white oak [green], chestnut oak [blue] and yellow-poplar [orange]. The red square inset delineates the study area.

Table 1 – Site information of chestnut oak and white oak populations used in this study. Populations marked with an * represents data available through the International Tree-Ring Data Bank: http://www.ngdc.noaa.gov/paleo/treering.html. Species abbreviations are: QUAL = white oak; QUPR = chestnut oak. Collectors were made by: LDEO = Tree-Ring Lab of Lamont-Doherty Earth Observatory of Columbia University; Wooster = Dr. Greg Wiles of the Tree-Ring Lab of the College of Wooster; McCarthy = Dr. Brian McCarthy of Ohio University; Baker = Dr. Patrick Baker of Monash University, Australia; and Duvick = Dr. Daniel Duvick of Iowa State University. Populations with [a] = includes trees cored in 1967 by Eugene Estes.

Site	Population	Species	Lat. (N)/ Long. (W)	# of Trees	Chronology Interval	Collector
1	Cranbrook Institute, MI*	QUAL	42.40/ -83.25	13	1581-1983	LDEO
2	Pulaski Woods, IN*	QUAL	41.03/ -86.42	11	1692-1985	LDEO
3	Andrew Johnson Woods, OH*	QUAL	40.53/ -81.45	35	1605-2000	LDEO/ Wooster
4	Dysart Woods, OH*	QUAL	39.59/ -81.00	10	1625-1988	McCarthy
5	Sigrist Woods, OH	QUAL	40.90/ -81.60	11	1663-2002	Wooster
6	Stebbins Gulch, OH*	QUPR	41.33/ -81.16	16	1609-1983	LDEO
7	Cook Forest, PA*	QUAL	41 21.207/ -79 14.677	18	1660-1981	LDEO
8	Prospect Mountain, NY	QUAL	43 25.300/ -73 34.200	18	1659-2001	LDEO
9	Schunnemunk Mountain, NY*	QUAL	41.23.692/ -74.6.674	25	1648-2001	LDEO
10	Goose Egg Ridge, NY	QUAL	43 04.100/ -73 17.400	20	1704-2002	LDEO
11	Goose Egg Ridge, NY	QUPR	43 03.760/ -73 17.890	21	1666-2002	LDEO
12	Middleburgh Talus, NY	QUPR	42 36.515/ -74 19.089	23	1674-2002	LDEO
13	Montgomery Place, NY	QUPR	42 00.682/ -73 55.244	20	1727-2002	LDEO
14	Mohonk Preserve, NY*	QUPR	41 45.828/ -74 07.479	50	1655-2002	LDEO
15	Hutchinson Forest, NJ*	QUAL	40.30/ -74.34	23	1620-1982	LDEO
16	Uttertown Bog, NJ	QUPR	41 06.942/ -74 25.004	29	1577-2002	LDEO
17	Otter Creek, PA*	QUPR	39 52.690/ -76 23.274	40	1578-2003	LDEO

Site	Population	Species	Lat. (N)/ Long. (W)	# of Trees	Chronology Interval	Collector
18	Otter Creek, PA	QUAL	39 53.000/ -76 23.385	19	1755-2003	LDEO
19	Savage Mountain, MD	QUPR	39 30.801/ -79 06.955	33	1646-2003	LDEO
20	Savage Mountain, MD	QUAL	39 31.015/ -79 07.577	19	1627-2003	LDEO
21	Cedar Knob, WV	QUPR	38.39/ -79.23	22	1660-2000	LDEO
22	Potomac River, VA	QUPR	39 3.487/ -77 19.795	18	1740-2003	LDEO
23	Blue Ridge Parkway, VA*	QUPR	37 32.757/ -79 27.951	29	1587-2002	LDEO
24	Patty's Oaks, VA*	QUAL	37 32.186/ -79 29.693	28	1520-2002	LDEO
25	Pinnacle Point, VA*	QUAL	38.30/ -78.21	17	1612-1981	LDEO
26	Watch Dog, VA*	QUPR	38.30/ -78.21	16	1642-1981	LDEO
27	Irish Creek, VA	QUAL	37 40.528/ -79 17.282	15	1687-2002	LDEO
28	Irish Creek, VA	QUPR	37 40.492/ -79 17.048	15	1594-2002	LDEO
29	Mountain Lake, VA*	QUAL	37.23/ -80.30	15	1552-1983	LDEO
30	Joyce Kilmer Forest, NC*	QUAL	35.13/ -83.58	23	1641-1983	LDEO
31	Linville Gorge, NC*	QUAL	35.53/ -81.56	20	1617-1977	LDEO
32	Little Scaly Mountain, NC	QUAL	35 1.894/ -83 15.476	18	1599-2003	LDEO
33	Bent Creek, NC	QUPR	35 30/ -82 37.5	22	1716-1996	Baker
34	Bent Creek, NC	QUAL	35 30/ -82 37.5	16	1688-1996	Baker
35	Norris Dam State Park, TN*	QUAL	36.13/ -84.05	34	1633-1980	Duvick
36	Piney Creek Pocket Wilderness, TN*	QUAL	35.42/ -84.53	11	1651-1982	Duvick
37	Lily Cornett Tract, KY*	QUAL	37.05/ -83.00	25	1660-1982	LDEO
38	Mammoth Cave, KY*[a]	QUAL	37.11/ -86.06	25	1649-1985	LDEO

Site	Population	Species	Lat. (N)/ Long. (W)	# of Trees	Chronology Interval	Collector
39	Sipsey Wilderness, AL*	QUAL	34.20/ -87.27	14	1679-1985	LDEO

Table 2 – Site information of yellow-poplar populations used in this study. Populations marked with * represents data available through the International Tree-Ring Data Bank: http://www.ngdc.noaa.gov/paleo/treering.html. Collectors were made by: LDEO = Tree-Ring Lab of Lamont-Doherty Earth Observatory of Columbia University; AR-TRL = Tree-Ring Laboratory of Arkansas University; and Duvick = Dr. Daniel Duvick of Iowa State University.

Site	Population	Lat. (N)/Long. (W)	Trees	Interval	Collector
1	Montgomery Place, NY	42.01/ -73.92	17	1754-2002	LDEO
2	Mohonk Preserve, NY	41.81/ -74.10	16	1865-2002	LDEO
3	Uttertown Bog, NJ	41.11/ -74.42	18	1732-2003	LDEO
4	Greenbrook Sanctuary, NJ	40.92/ -73.93	13	1750-2000	LDEO
5	Otter Creek, PA	39.88/ -76.39	9	1764-2002	LDEO
6	Fiddler's Green, VA	41.39/ -74.11	20	1668-2002	LDEO
7	Rainbow Falls, TN*	35.40/ -83.30	6	1796-1995	AR-TRL
8	Porter's Creek, TN*	35.40/ -82.23	13	1698-1997	AR-TRL
9	Boogerman Trail, TN*	35.36/ -83.05	11	1736-1995	AR-TRL
10	Scott's Gap, TN*	35.36/ -83.55	14	1684-1981	Duvick
11	Joyce Kilmer, NC*	35.21/ -83.55	7	1672-1997	AR-TRL

(Gower et al., 1996). Our data represent new data for important species of the eastern deciduous forest (Burns and Honkala, 1990).

The smaller yellow-poplar network is included to contrast species with different life-history traits. Chestnut oak and white oak trees tolerate lower light conditions in the understory better than yellow-poplar, a gap-obligate species (Burns and Honkala, 1990; Orwig and Abrams, 1994). Yellow-poplar is also the tallest hardwood tree in the eastern U.S. (Burns and Honkala, 1990). Because of these traits, only in rare cases would mature yellow-poplar experience increased growth rates as the result of reduced canopy competition.

Oaks were sampled during two time periods: from the late-1970s through the 1980s and the late-1990s through 2003 with the exception of trees sampled at Mammoth Caves, KY in 1967. Nine of the 11 yellow-poplar populations were sampled between the late-1990s to early-2000s, with the remaining yellow-poplar sampled in 1982. One to two increments cores were collected per tree in all collections. Collections made for this study (populations whose last year is 2000 A.D. or later except for A.J. Woods, OH and Cedar Knob, WV) were more ecologically oriented than standard dendroclimatological collections: canopy trees across a range of size and age classes were selected for coring and diameter at breast-height (DBH) was recorded for each tree cored. The sampling strategy for the other collections focused primarily on coring the oldest trees to create long records of past climate. Core processing followed standard dendrochronological techniques (Cook and Kairiukstis, 1990). Multiple cores were averaged to create average radial increment per tree.

Oak species were combined and individual trees were grouped into six 50-year periods (innermost ring dating to pre-1651 A.D., innermost ring between 1651 and 1700 A.D., ...1851-1900 A.D.) to isolate the long-term growth trends of old trees. Average tree age of the oldest class is 375 years (min. = 319, max. = 464). Yellow-poplar was grouped into three 70-year periods (innermost ring dating to pre-1781 A.D., 1781-1850 A.D. and 1851-1920 A.D.) to have sufficient number of trees per class. Average age of the oldest yellow-poplar age class is 263 years (min. = 205, max. = 336). These groupings represent age classes, although some trees are older than their classification because ages represent age at coring height and the tree's center was located only in a minority of the cores.

Using average raw ring-width chronologies in this study would be misleading because of potential differences in tree and stand-level productivity at low sample depths. Such differences could lead to false conclusions of actual growth rates. To avoid this potential pitfall, differences in tree-scale productivity are removed using a horizontal straight-line curve fit through the mean of each time-series. The resulting time-series are standardized to a mean value of 1 following standard dendrochronological methods (Cook and Kairiukstis, 1990) and averaged to calculate the mean annual chronology for each age class. Multiplying the mean annual chronology by the average ring width of its corresponding raw ring-width chronology produced time-series of average radial increment (mm) (Esper et al., 2001). Two-tailed 95% bootstrap confidence limits were estimated from the average radial growth chronology for each age class (Cook, 1990). All time-series were smoothed with a 10-yr spline to emphasize decadal-scale variations and centennial-scale trends. These methods did not alter the long-term trend in ring width.

Results/Discussion:

Average ring widths of the two oldest oak age classes are significantly above the long-term mean throughout most of the 20th century (Figure 2a, b). The oldest age class

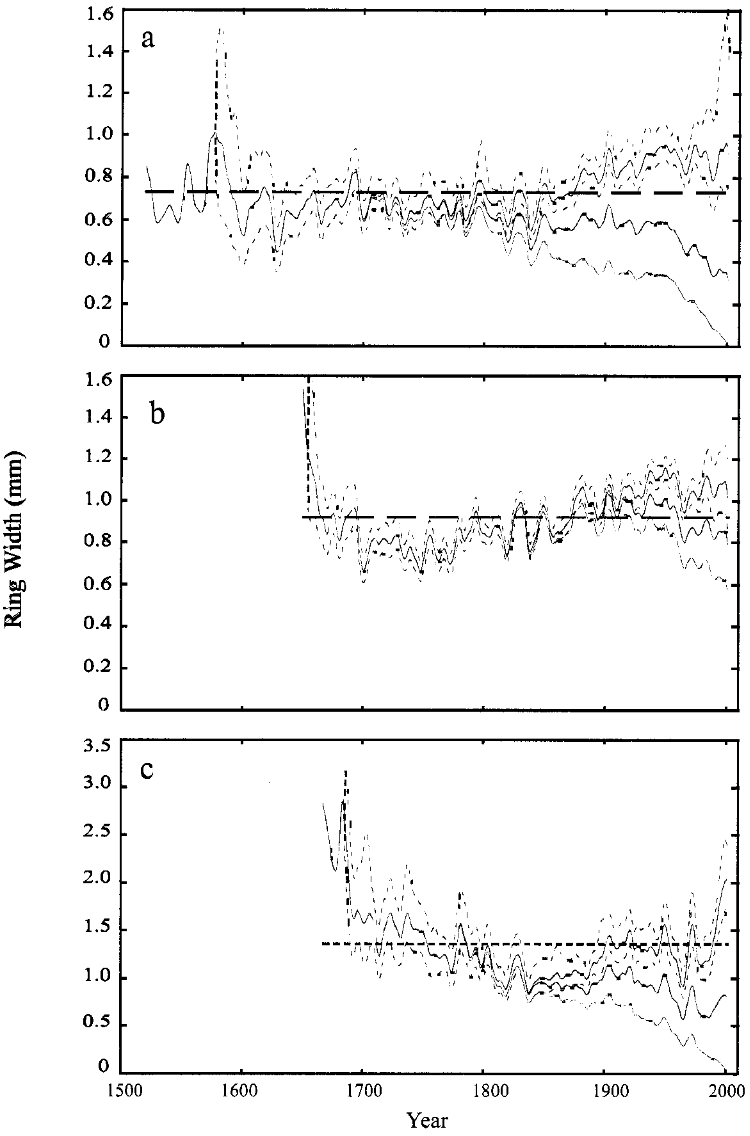

Figure 2 - Average raw ring widths for the two oldest oak classes (a = pre-1651 A.D., n = 48; b = 1651-1700 A.D., n = 162) and oldest yellow-poplar class (c = pre-1781 A.D., n = 34). The trend of increasing ring widths began in the late-1840s when trees in the oldest oak class averaged 261 years of age (201/346, min./max., respectively), which is 56% of their maximum known age (MKA). The large jump in yellow-poplar ring-widths in the late-1880s occurred when average tree age was 145 years old, which is 43% MKA. Average ring widths in the oldest oak and yellow-poplar age classes are significantly larger than modeled ring widths (see below) just prior to the trend of increased ring widths. The solid red line represents population mean. Dashed red lines represent the upper and lower 95% confidence limit. The horizontal dashed line represents the long-term mean. A blue line represents modeled ring widths based on decelerated growth rates beginning at 1/2 MKA while an orange line represents modeled ring widths based on decelerated growth rates at 1/3 MKA. Bootstrap confidence limits were calculated for modeled ring widths, but are not shown to improve figure clarity. All time-series are smoothed with a 10-yr spline to emphasize decadal-scale variations and centennial-scale trends. Note: the Y-axis for yellow-poplar has a different scale.

has a trend of increasing ring widths beginning in the late-1840s that becomes significantly above the mean starting in the 1880s. On average these trees were more than one-half MKA in the 1880s. A trend of increasing ring widths is present in the next oldest age class over a 180-year period and raw ring widths are significantly above the mean after 1875. All oaks, except for the 1851-1900 class, exhibit a similar pattern of ring width variation: initially large rings followed by ring widths less than or equal to the mean, followed by an upward trend beginning in the mid-1800s. Oaks with inner ring dates after 1801 have ring-width trends that are different than the oldest oaks. However, these variations should be interpreted cautiously because most of these trees are distributed primarily in the northeastern end of the study area. The trend of increasing ring widths since the mid-1800s of the four oldest oak age classes best represents the entire study area (Figure 3a-d). These trends also hold true at the population level (Figure 4).

The oldest yellow-poplar age class has the often-expected trend of declining ring widths after recruitment for shade-intolerant species (Figure 2c). The trend is reversed after 1885 and ring widths are significantly above the long-term mean in the late-1940s to early 1950s, early 1970s and after 1992. Significantly below average ring-widths in the 1960's are most likely associated with drought, which reduced tree growth throughout the eastern United States (Cook, 1991). The 1781-1850 A.D. class of yellow-poplar has a strikingly similar pattern in ring width variation (Figure 3e, f).

Increasing ring widths around an expanding stem diameter implies a substantial increase in growth rates. To quantify the trend in terms of growth rates and carbon uptake, allometric equations were used to convert ring-width series to biomass. Time-

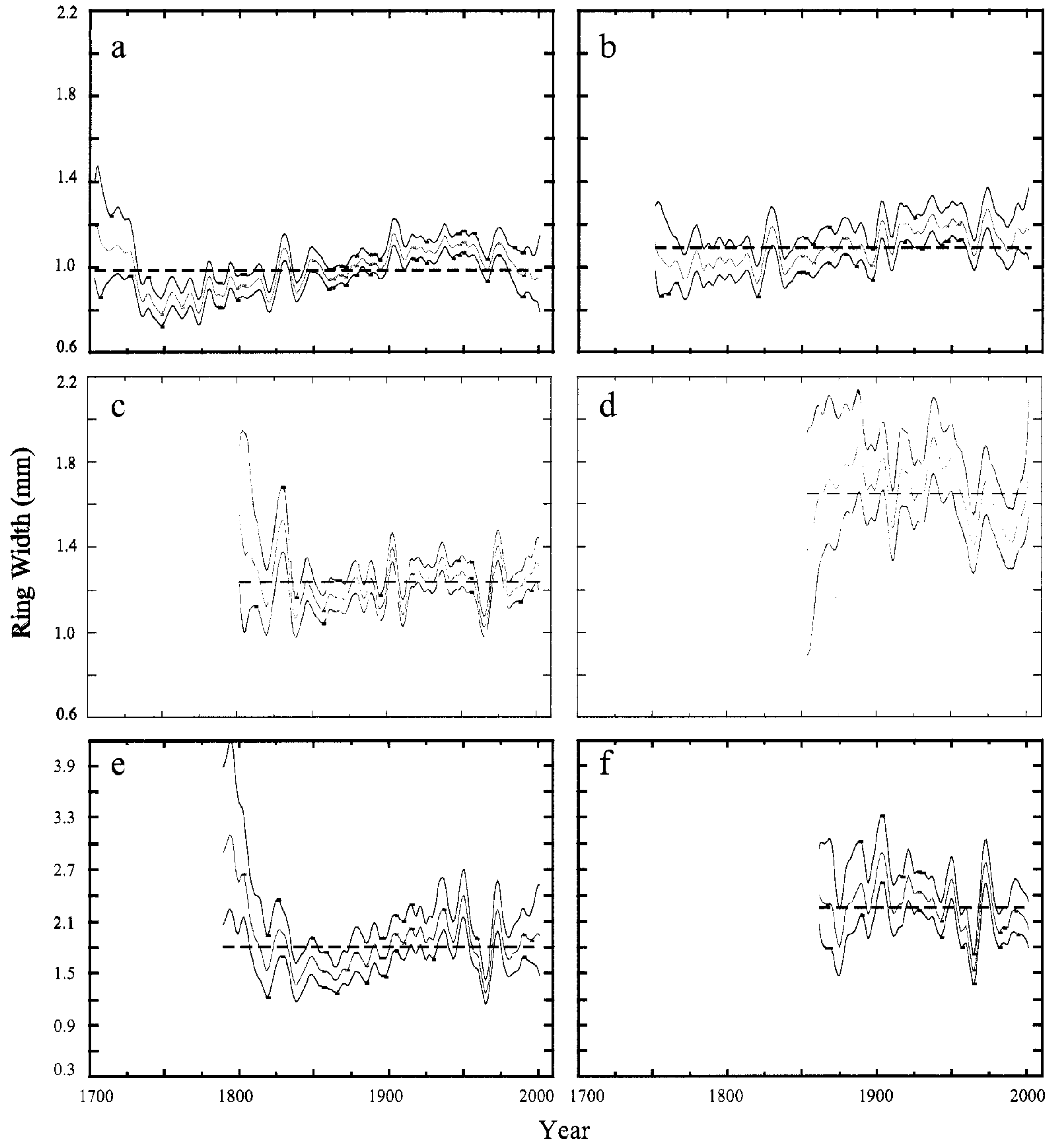

Figure 3 - Raw ring width chronologies of oak age classes with inner ring dates after 1700 (a-d) and the youngest yellow-poplar age classes (e, f). The three oldest oak age classes in this figure show increasing raw ring-widths since the mid-1800s (a = 1701-1750 A.D., n = 187; b = 1751-1800 A.D., n = 183; c = 1801-1850 A.D., n = 171). The 1781-1850 A.D., yellow-poplar age class has the same trend (e; n = 44). Only the youngest oak (d = 1851-1900 A.D., n = 86) and yellow-poplar (f = 1851-1920, n = 66) classes do not show the same long-term trend in ring width. They do, however, have periods of above-average ring widths in the 1900s. The dashed line represents the long-term mean. Orange line represents population mean. Blue lines represent the upper and lower 95% confidence limit. All time-series are smoothed with a 10-yr spline to

emphasize decadal-scale variations and centennial trends. Note: the y-axis for yellow-poplar has a different scale.

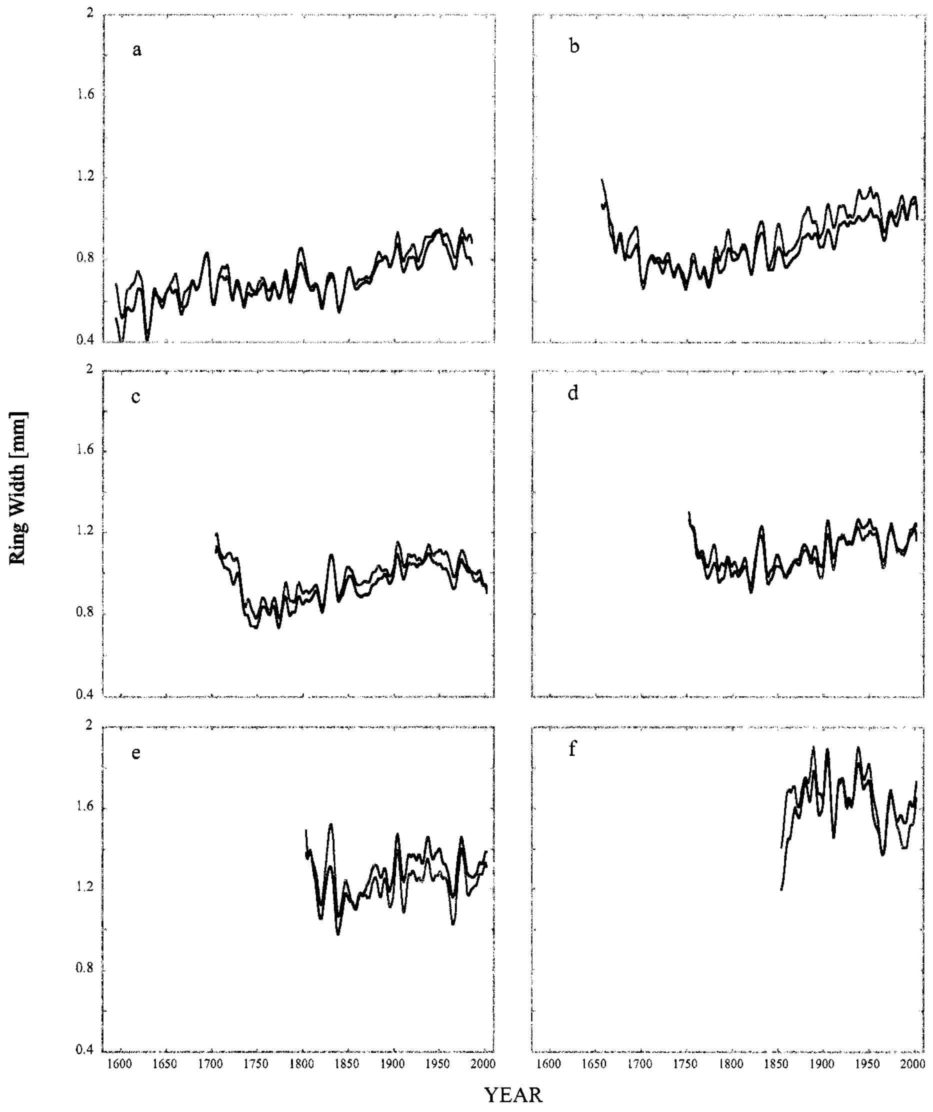

Figure 4 - Comparison of average ring-widths for all oak classes at the individual-tree (orange line) and population level (blue line): This figure compares average ring-width trends of all oaks across the entire study area versus average of each oak population for each age class. There is no significant difference between tree-level and population-level radial ring widths. To calculate the time-series of average ring widths at the population level, radial growth of all trees from a population (i.e. Cranbrook Institute, Table 1) were first averaged for each age class. The population-level raw ring width chronologies were then averaged across the study region. All time-series are smoothed with a 10-yr spline to emphasize decadal-scale variations and centennial-scale trends. (age classes are: A = pre-1651 A.D.; B = 1651-1700 A.D.; C = 1701-1750 A.D.; D = 1751-1800 A.D.; E = 1801-1850 A.D.; F = 1851-1900 A.D.).

series of average raw ring width for each age class were used to reconstruct the annual inner-bark diameter at breast height. The reconstructed diameter represents the average stem diameter for each age class. The average annual diameter for each age class was placed into an allometric equation for white oak (to represent white oak and chestnut oak) or yellow-poplar to calculate annual aboveground biomass (Ter-Mikaelian and Korzukhin. 1997). MIC was calculated by multiplying the aboveground biomass chronology by 0.498 (Birdsey, 1992).

Growth rates are expressed as the mean annual increment of aboveground carbon per tree (MIC) for each age class. MIC increased through time for all species and age classes, except for the 1701-1750 age class of oaks (Figures 5, 6). This age class, however, had the same trend of carbon uptake until a recent period of relatively constant growth. Nonetheless, the remaining trees of all species, including the oldest, attained their highest growth rates in the most recent decades.

Age is not the primary factor limiting individual tree growth in this study. Separating trees into age classes did not diminish long-term growth trends. In fact, the opposite is observed: average growth rates in the oldest age classes accelerated at more than 300 and even 400 years of age. Most trees experienced increased growth rates at over 150 years of age. Even the oldest-known individuals of each species have a trend of increasing ring widths since the mid-1800s and have some of their widest rings at more than 95% MKA (Figure 7).

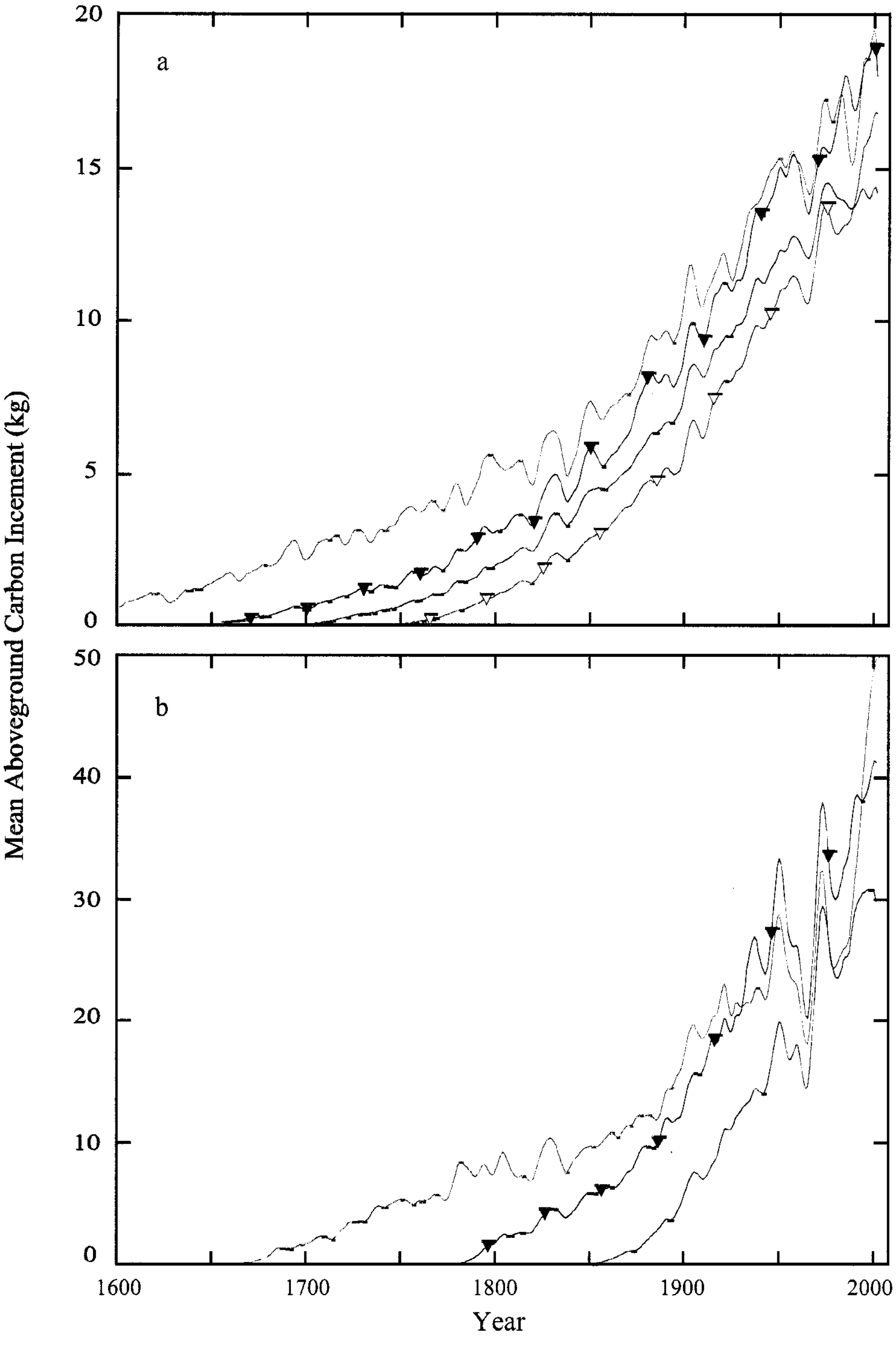

Figure 5 - Mean annual increment of aboveground carbon per tree (MIC) by size class (diameter at breast height) for (a) oak and (b) yellow-poplar. All oaks show increasing productivity with the largest trees showing the greatest increase in growth rates over the last 150 years (size classes are: dark red = < 39 cm, n = 36; red = 40-49 cm, n = 66; orange with inverted hollow triangles = 50-59 cm, n = 84; purple with dotted circles = 60-69 cm, n = 62; purple = 70-79 cm, n = 47; blue with inverted hollow triangles = 80-89 cm, n = 17; light blue = 90+ cm, n = 9). Yellow-poplars experienced increasing

productivity across all size classes as well, with the largest classes having the increase in growth rates in the last 100 years (size classes are: dark red = <59 cm, n = 24; green = 60-79 cm, n = 37; blue = 80+ cm, n = 25).

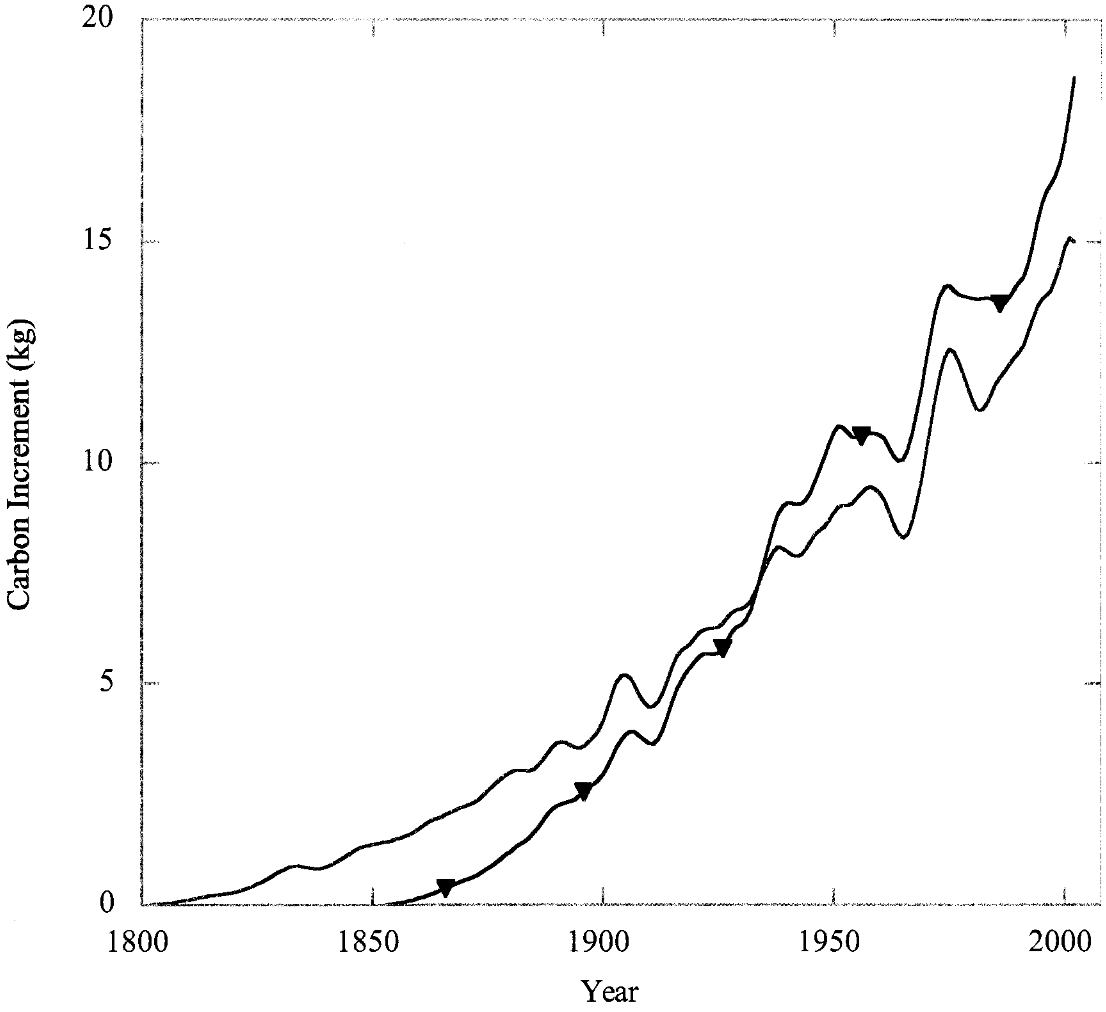

Figure 6 - Mean annual increment of aboveground carbon per tree of the two youngest oak age classes. Both age classes show accelerated growth over the last 150 years. The orange line represents oaks with an inner ring between 1801-1850 A.D. The blue line with inverted triangles represents oaks with an inner ring between 1851 and 1900 A.D. Both curves were smoothed as described in Figure S2.

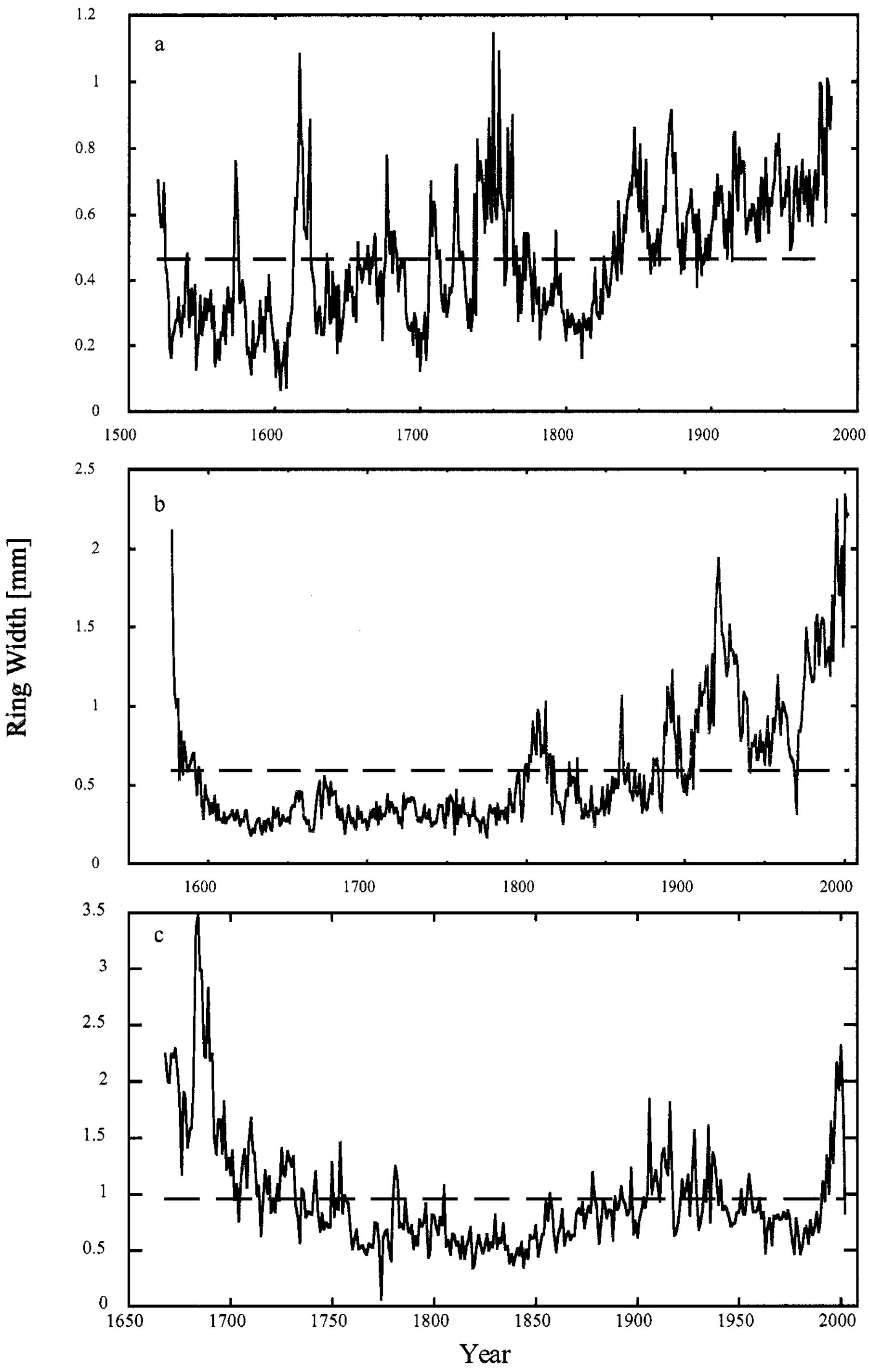

Figure 7– Time-series of raw ring widths of the oldest-known white oak (a), one of the two oldest-known chestnut oaks (b) and oldest-known yellow-poplar (c). Each tree has some of their largest rings in the decade immediately prior to sampling. The horizontal dashed line represents the mean ring width for each tree. Note: the X and Y-axes for each tree are different.

To emphasize the unexpected increase of ring widths at old ages, hypothetical models of ring width were built based on the assumption of declining growth rates as trees age (Clark, 1990; Wykoff, 1990) We wanted to compare the trend of increasing ring widths of the oldest oak and yellow-poplar age classes to ring widths of modeled trees under the assumption that growth rates decline as trees age (following Clark (1990) Figure 8; and Figure 1 in Wykoff (1990)). The common assumption of individual tree growth may be best summarized in Wykoff (1990), p. 1079:

"Diameter increment increases to a maximum early in the life of a tree and then slowly decreases, approaching zero as the tree matures."

Based on these concepts of individual-tree growth, allometric equations were used to 'hind cast' ring widths based on annual increments of biomass production. Average growth rates of the two oldest oak age classes and the oldest yellow-poplar age class were decelerated beginning at one-third and one-half maximum known age (Figure 8). The first model decelerates growth rates beginning at one-third MKA (LOWER). Goals of the LOWER model were to have growth rates peak around 50% of MKA, stay constant until 75-90% of MKA, begin a decline at 90% MKA and have rates fall to near zero at MKA. The second model (UPPER) decelerates growth rates beginning at one-half MKA. Goals of this model were to have growth rates that peak around 75% MKA and then hold relatively steady until a decline beginning at 90% MKA. The LOWER model represents a lower expectation of growth rates while the UPPER model represents an upper limit. Given the prevailing assumptions of individual-tree growth rates, both models could be considered conservative models.

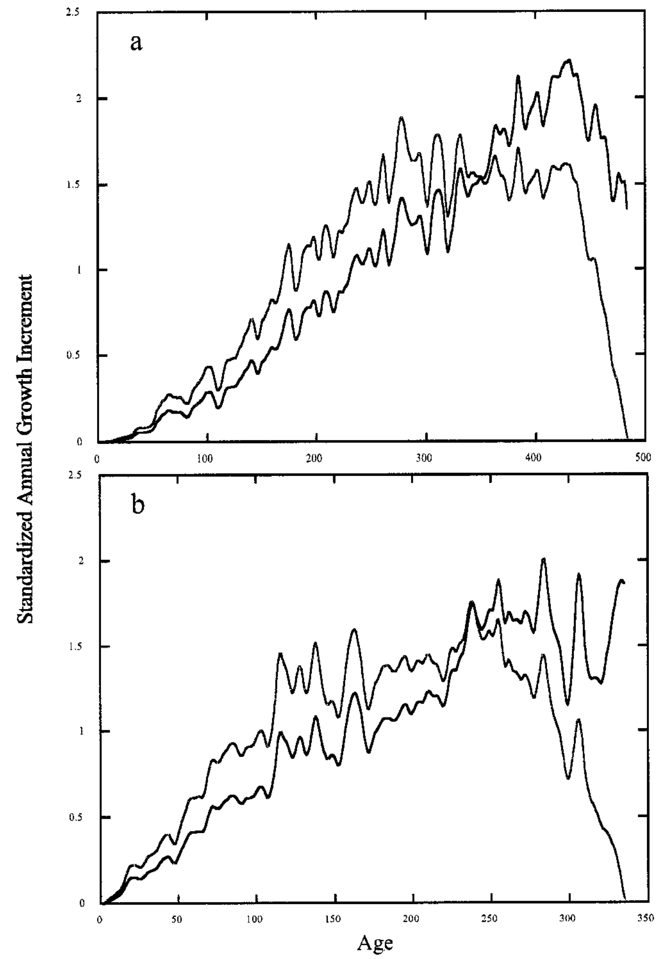

Figure 8 – Two models representing an upper and lower expectation of annual growth for oak (a) and yellow-poplar (b). Annual growth rates of the LOWER oak model increase and peak at 277 years (57% of MKA) (orange line in **a**) and were essentially constant for at least 150 years. Annual growth rates of the UPPER oak model accelerate until reaching a peak at 431 years (89% MKA) (blue line in **a**). Annual growth increments of the LOWER yellow-poplar model increase and peak at 240 years (71% of MKA) (orange line in **b**). Annual growth rates for this curve, however, are nearly constant between 110 and 230 years (33 and 68% MKA). The steep decline in growth rates around 290 (86% MKA) years is partly caused by their strong response to the 1960s drought (see the main text for details). Annual growth rates of the UPPER yellow-poplar model accelerate and peak at 283 years (84% MKA) (blue line in **b**). Growth rates are relatively constant between 240 and 300 years (71 and 89% MKA). All time-series are smoothed with a 10-yr spline to emphasize decadal-scale variations and centennial trends. Note: the scale of the yellow-poplar X-axis is shorter than for oak.

Actual growth rates were, on average, reduced annually for the LOWER model by 0.25% for oak (range = 0.1%-0.5%/year) and 0.41% for yellow-poplar (range = 0.2%-

0.6%/year) prior to declining at 90% MKA. After 90% MKA, growth rates were decelerated by 0.5% for oak and 0.64% for yellow-poplar annual. For the UPPER model actual growth rates were reduced annually by 0.35% for oak and 0.44% for yellow-poplar prior to declining at 90% MKA. Growth rates of the UPPER models were also decelerated by 0.5% for oak and 0.64% for yellow-poplar after 90% MKA. This method of modeling preserves decadal-scale variation and only alters long-term trends.

The peak of annual growth rates in the model trees, however, does not match our stated goals. Annual growth rates of the LOWER oak model increase and peak at 277 years (57% of MKA) (orange line in Figure 8a) and were essentially constant for at least 150 years. Annual growth rates of the UPPER oak model accelerate until reaching a peak at 431 years (89% MKA) (blue line in Figure 8a). Goals of the hypothetical growth rates for yellow-poplar were more difficult to attain. Annual growth increments of the LOWER model increase and peak at 240 years (71% of MKA) (orange line in Figure 8b). Annual growth rates for this curve, however, are nearly constant between 110 and 230 years (33 and 68% MKA). The steep decline in growth rates around 290 (86% MKA) years is partly caused by their strong response to the 1960s drought (see the main text for details). Annual growth rates of the UPPER yellow-poplar model accelerate and peak at 283 years (84% MKA) (blue line in Figure 8b).

Growth rates are relatively constant between 240 and 300 years (71 and 89% MKA). (Figure 8). Annual growth rates of the oldest oak and yellow-poplar age classes were slightly reduced (0.1% - 0.64%/yr) beginning at one-third (LOWER) and one-half (Upper) MKA to model lower and upper expectations of growth over the lifespan of a tree. Ring widths of the LOWER oak model are significantly smaller than the oldest oak class after 1805 (59% MKA), even though MIC peaked at 57% MKA and was held relatively constant until 90% MKA. Ring widths of the more conservative UPPER oak model are significantly narrower than the oldest oaks after 1836 (65% MKA), despite increasing MIC that peaked at 89% MKA. Hypothetical ring widths of the UPPER model for the second oldest oak age class were significantly smaller than the real ring widths from 1937-1986. Ring widths of the conservative UPPER yellow-poplar model, whose MIC peaked at 84% MKA, are significantly narrower than the oldest yellow-poplar after 1916. Remarkably, modeled ring widths were smaller than actual ring widths despite being formed around smaller stem diameters. If modeled trees were allowed to reach the final size of the actual trees through faster initial growth rates, modeled ring widths at old ages would be even narrower than the models used in our analysis. This experiment suggests that ring width is a sensitive indicator of changes in aboveground biomass production.

Early tree physiology models considered cambial growth as secondary growth. A more contemporary carbon allocation model suggests that allocation to cambial growth follows allocation to new foliage, buds, roots and non-structural storage (Waring and Pitman, 1985). If these physiological requirements are to be met prior to full cambial expansion, the oldest oak and yellow-poplar trees could be considered as growing vigorously. This inference is in line with a study demonstrating that there is no statistical difference in the physiological activity of bristlecone pine meristem in trees ranging from 23-4713 years (Lanner and Conner, 2001). The increase in ring widths of the old trees also supports a controlled study indicating that old trees can respond to an improved growth environment (Latham and Tappeiner, 2002). Together, these results suggest that trees can persist in the landscape while maintaining the ability to respond vigorously to improved growth conditions at old ages, which could be evolutionarily advantageous.

Because old trees are survivors of multi-centennial competition, they may represent a survivorship bias. Likewise, old trees sampled for dendrochronological research may represent a modern bias. For example, old trees may have grown slower initially than cohorts that have since died out of the landscape. Older boreal conifers were generally found to have narrower average ring-widths of the first 100 years than younger trees (Melvin, 2004). The same relationship is found in our oak data. Like Melvin (2004), a significant relationship is found between the average ring-width of the first 100 years and age of the each oak tree ($n = 147$) at coring height at the time of sampling ($y = 367.9 - 111.1x$; $r = 0.629$). This relationship indicates that the oldest (youngest) trees at the time of coring had the narrower (wider) average ring-widths in the first 100 years after reaching coring height. Only oaks with the pith present in at least one core were used for this analysis because the presence of a tree's pith is the only reliable way to determine the true age of each tree at coring height in closed-canopied forests. Even if the oldest trees sampled represent a biased population, however, increased growth rates in these trees contradict most expectations of tree growth and has important implications for carbon sequestration.

Recently sampled oak and yellow-poplar were divided into size classes to test the hypothesis of a size-related decline of growth rates. The size-related decline hypothesis was tested on trees sampled by the first author. We were unable to locate DBH data from trees collected during the earlier sampling period. DBH data from earlier collections does not exist in most cases. Oaks were divided into 10 cm diameter at breast height (DBH)

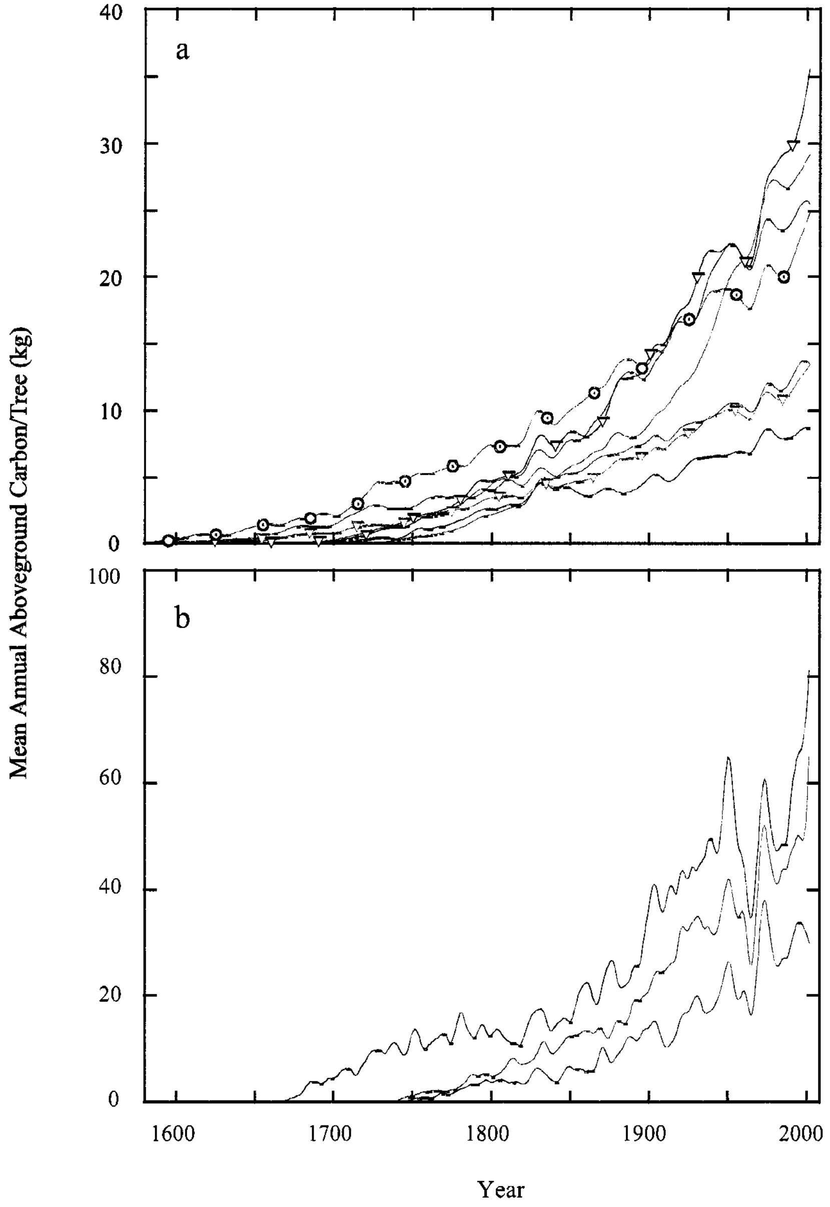

Figure 9 - Mean annual increment of aboveground carbon per tree (MIC) for the (a) four-oldest oak age classes (an inner ring prior to 1801) and (b) all yellow-poplar age classes. Each oak class has increasing productivity except for the 1701-1750 A.D. group, which is relatively constant over the last 40 years (orange line = pre-1651 A.D.; blue line with inverted triangles = 1651-1700 A.D.; red line = 1701-1750 A.D., n = 187; green line with hollow triangles = 1751-1800 A.D., n = 183). All yellow-poplar age classes experience increasing productivity, including a sharp increase prior to 1900 (orange line = pre-1781 A.D., blue line with inverted triangles = 1781-1850 A.D., n = 44; red line = 1851-1920 A.D., n = 66). MCI was calculated using published allometric equations for white oak (for both oaks) and yellow-poplar. All time-series are smoothed as in Figure 2. Note: the Y-axis for yellow-poplar has a different scale.

classes while yellow-poplar was divided into 20 cm classes to maintain higher sample replication per size class. Time-series of MIC were calculated using the same method for the age class analysis.

Unexpectedly, growth rates increased in the largest trees and increased more rapidly in larger trees than smaller trees (Figure 9). Differences in growth rates between oaks >90 cm DBH and <39 cm are not related to age structure. The oldest trees in these size classes date to the early 1700s and ~ 90% of the trees are present in each chronology by 1840. While this database is limited, these results contradict predictions of the size-related growth decline hypothesis.

Our data shows increased individual-tree growth rates over nearly 400,000 km^2 in temperate eastern North America, a region with a large and dynamic aboveground carbon pool (Myneni et al., 2001). The increased growth rates of all 981 trees coincide temporally with increased tree growth rates in many regions globally (e.g., Briffa, K.R. 1992; Becker et al., 1995; Rolland et al., 1998; Esper et al., 2001; McKenzie et al., 2001; Villalba et al., 2003). Most of these trees grew at high latitude or elevation where increased tree growth rates have been associated with warming. New research, however, suggests that there may be more long-term trends in precipitation over the last two centuries than previously recognized (Wilson et al., 2005). As drought is the primary limiting growth factor in most of our oak populations (Cook, 1991), accelerated growth rates could be readily explained if a similar trend in drought exists in our study region.

Life history traits of yellow-poplar dictate that nearly all of the oldest yellow-poplar were canopy dominants by 1850. Therefore, the trend in growth rates is most likely caused by an exogenous factor, not stand dynamics. If increased growth rates are caused by stand dynamics, it suggests models of tree and stand development in closed canopied forests need to be reconsidered. Our data indicates that growth rates of old trees in natural forests do not peak in annual growth rates until they are more than 75% MKA. Because many factors (such as elevated CO_2, elevated nitrogen deposition, climate change, competition, etc.) could be contributing to increased growth in the eastern United States, it is beyond the scope of this study in determining what is driving increased growth rates. It should be noted, however, that the trend of increased growth begins well before the loss of the American chestnut (*Castanea dentata*) and substantially increased levels of atmospheric CO_2 and nitrogen deposition.

Conclusion:

We found increased growth rates in trees of the oldest age classes and the oldest-known individuals of three species over the last 150 years. Combined with evidence from other studies, these results suggest that tree-level productivity does not always decline with age. Results of our age-related and size-related analysis suggest that if old forests do experience age-related declines in growth rates, factors other than individual-tree growth must be the cause (Binkley et al., 2002).

Because these results are in opposition to the long-held tenet that growth rates decline as trees age, it suggests that old-growth forests could be active carbon sinks (Schulze et al., 2000; Carey et al., 2001). Furthermore, our data extends previous findings into new, widespread and important forested ecosystems and can serve as a model for the increasingly common 100-180+ year old forests in temperate eastern North America. Temperate forests have been shown to have the strongest age-related increase in living biomass and total ecosystem carbon (Pregitzer and Euskirchen, 2004). Our data extends this finding with a similar age-related increase in tree growth rates. At the very least, our data shows that old trees can be a vital element of the terrestrial carbon cycle. The potential for old trees to respond to improved growth conditions has implications for carbon sequestration, tree and forest modeling, tree-ring analysis of trees in closed-canopied forests, ecosystem management and evolution.

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Climatic Sensitivity and Growth of Southern Temperate Species in the Eastern U.S.

My dissertation research focused on three primary questions: 1) "*Is temperature an important factor of the growth rates of southern temperate tree species*?", 2) "*What are the biotic and abiotic factors influencing tree growth rates/carbon uptake*?" and 3) "*Have tree growth rates changed significantly over the past two centuries*?" Each dissertation chapter and appendix addressed at least one of these questions and often, more than one.

Winter temperatures are consistently the most important temperature factor of southern tree growth (Pederson et al., 2004; Chapter 2; Hopton and Pederson, in press; Chapter Three; Appendix A). The common winter temperature response along the NE/NY ecotone is consistent with the hypothesis that winter temperatures control ecotone position (Neilson, 1993). Further, winter temperatures appear to be a significant factor of tree growth across much of temperate North American (Brubaker, 1980; Conkey, 1982; Tainter et al., 1984; Cook et al., 1987, 2001; Pan et al., 1997; Rubino and McCarthy, 2000; Naidoo and Lechowicz, 2001; D'Arrigo et al., 2001; Tardif et al., 2001). Results presented here together with prior studies reveal an emerging of a significant relation between winter temperatures and tree growth in temperate North America.

Atlantic white-cedar (AWC) is the most temperature sensitive species studied here (Pederson et al., 2004; Chapter 2; Hopton and Pederson, in press; Appendix A). Its temperature sensitivity compares well to red spruce (*Picea rubens* Sarg.), the species used for the only temperature reconstruction in the northeastern U.S. (Conkey, 1982).

The red spruce reconstruction was based on wood density, however. AWC currently holds the greatest potential for a reconstruction of annual temperatures for the Boston, MA and New York City, NY region from ring widths because of the loss of temperature response in red spruce during the last half of the 20th century (Cook and Johnson, 1989). As many AWC forests in the northeast U.S. were logged in the late-1800s, recovery of subfossil AWC wood from wetlands or material from old buildings is necessary to produce a reconstruction of temperature longer than regional meteorological records.

Potentially important differences in the temperature growth response were revealed between: 1) Atlantic white-cedar, 2) pitch pine, 3) white oak, 4) chestnut oak, 5) northern red oak and 6) pignut hickory. Atlantic white-cedar and pitch pine are more sensitive to winter temperatures than white oak, chestnut oak, northern red oak and pignut hickory in the Hudson River Valley of New York State (HRV). This finding is in agreement with a study in the upper Great Lakes of Michigan, which showed pines to be more sensitive to temperature than hardwood trees (Graumlich, 1993). Also, pitch pine and AWC growth in the HRV correlates to a longer season of winter temperatures than the hardwood species, which should benefit these coniferous species more than the hardwoods as winters become shorter. Differences in temperature sensitivity also exist at the subgenus level. Leucobalanus (white oak group as represented by white oak and chestnut oak) are more sensitive to temperature than Erythrobalanus (black oak group as represented by northern red oak) (Pederson et al., 2004; Chapters 2, 3). Similar differences were found between these subgenera in an ecophysiological study in northern Florida (Cavender-Bares and Holbrook 2001) and a dendrochronological study across a drought gradient in the southeastern U.S. (Cook et al., 2001). Many of the differences in temperature response of tree growth found as a part of this dissertation research occur at the margins of the growing season or during the non-growing season. For example, growth of pignut hickory is significantly correlated to late growing-season temperatures, which is unique for the six species studied in the HRV (Pederson et al., 2004; Chapter Two). Also, tree growth at the oak-hickory ecosystem level is significantly related to prior-October temperatures. Temperature is thought to be an important factor in the phenology of the temperate forest (Kramer et al., 2000). Differing temperature responses between species likely reflect their differing phenologies.

Climatic sensitivities were also shown to change across geographic scales. For example, northern populations of the AWC are more temperature sensitive than southern populations (Hopton and Pederson, in press; Appendix A). In contrast, January temperatures most significantly constrain tree growth of the oak-hickory ecosystem and the Leucobalanus subgenus in the southern half of the HRV. Finally, NRO has a tendency to be limited by late-summer temperatures at northern-range-margins and in central New England (Chapter 3). These findings are consistent with prior research showing that a species' climatic response changes with geographic location (Cook and Cole, 1991; Cook et al., 1998; LeBlanc and Terrell, 2001). Geographic locations, therefore, has an importance role in the temperature response of tree species.

Despite research showing that the climate response of multiple species can be statistically condensed to a few phenotypes (*i.e.,* Graumlich, 1993; Cook et al., 2001), the minor differences in temperature sensitivity between species may be biologically significant. Phenology is thought to be an important contributor to species distribution (Chuine and Beaubien, 2001). Phenology is also hypothesized to be an important contributor to a species' response to climate change (Kramer et al., 2000), which could result in important differences in ecosystem productivity. Given the large number of canopy tree species in the southern Appalachians that are forecast to benefit from climatic warming (Iverson and Prasad, 1998), it seems important to continue species-level studies so that the impact of future climate change can be better anticipated.

Drought has also previously been shown to be a dominant growth factor of tree growth in the eastern U.S. (Cook et al., 1999), including for half of the oak populations studied in Chapter Three (Cook, 1991). Drought typically accounts 20-50% of the annual variance in ring width (Cook et al., 1999) while temperature explained <10% of the annual growth for white oak, chestnut oak, northern red oak and pignut hickory (Pederson et al., 2004; Chapters 2, 3) and 20-30% for AWC (Pederson et al., 2004; Chapter 2; Hopton and Pederson, in press; Appendix A). Drought is the most dominant and consistent climatic limitation of northern red oak growth (Chapter Three). NRO's positive correlations to June and July precipitation and negative correlations to temperatures during the same months reflect its evapotranspirational demand during early summer in the northeastern U.S. The growth response of yellow-poplar to the mid-1960s drought was greater than for white oak and chestnut oak (Chapter 4). As white oak and chestnut oak are some of the most commonly used species of drought reconstruction in the eastern U.S. (Cook et al 1999), the stronger growth response of yellow-poplar suggests that it may be one of the more sensitive species to drought. These results highlight the need for more studies on the drought response at the tree species level.

Gypsy moth defoliation events had a significant impact on multi-annual growth of several species. Northern red oak, the focus of the gypsy moth defoliation analysis, showed a strong negative impact to defoliation (Chapter 3). Its strong negative response is related to the fact that it is more significantly impacted by gypsy moth defoliation the year after an event than most other species studied to date (Muzika and Liebhold, 1999). Red maple at the HF was also negatively impacted by the 1981 defoliation event. In fact, trend in growth rates of NRO and red maple since 1981 suggest the defoliation may have accelerated compositional changes in the HF. Ring characteristics and growth declines strongly suggest similar gypsy moth defoliation events in other species, most notably in the chestnut oak at Montgomery Place, Uttertown and the Mohonk Preserve and white oak population on Schunnemunk Mountain (N. Pederson, unpublished data). Evidence suggests, however, that forested ecosystems are adapting to gypsy moth (Campbell and Sloan, 1977; Muzika and Liehbold, 1999). If this is true, gypsy moth may become less of a factor unless synergy with climate change or other insects and pathogens increase its virulence.

Individual-tree growth rates of five species studied here increased over a significant portion of the eastern U.S. during the last 50-150 years. Increased ring widths since the mid-1800s occurred in chestnut oak, white oak and yellow-poplar over an area covering nearly 400,000 km^2 in the eastern U.S. (Chapter 4). When the ring widths of these trees are converted to aboveground carbon increment, it is clear that growth rates have accelerated over that time. Similarly, Atlantic white-cedar shows a substantial increase in the ring width index since the 1920s (Hopton and Pederson, in press; Appendix A), which also translates to increased growth rates (N. Pederson, unpublished data). Most of the 20 northern red oak populations sampled have increased growth rates over the last 50 years in the northeastern U.S. (Chapter 3). The consistency of these results over a wide range of site types, climatic regions and land-use histories suggests that increased tree growth rates must be an important factor to the terrestrial carbon sink in the eastern U.S.

The cause behind the increased growth rates is not clear for all species. Simulation models suggest that global primary productivity has increased as a result of improved climatic conditions (Nemani et al., 2003). Increased growth rates of AWC are strongly tied to winter and minimum spring and summer temperatures (Hopton and Pederson, in press; Appendix A). The changes in growth rates of chestnut oak, white oak and yellow-poplar occur temporally with increased tree growth rates at high latitudinal and elevational sites globally (e.g. Briffa, 1992; Becker et al., 1995; Jacoby et al., 1996; Rolland et al., 1998; Esper et al., 2001; McKenzie et al., 2001; Villalba et al., 2003). Many of the changes at high latitude and elevation are associated with warming. Because tree growth in the eastern U.S. is significantly correlated to winter temperatures, winter temperatures must be considered an important factor of increased growth rates, especially as they have steadily warmed since the late-1800s (Jones and Moberg 2003; Lugina et al., 2003). Recent work, however, also suggests that there may be more low-frequency variations in precipitation/drought than previously assumed (Wilson et al., 2005). If climate change in eastern New York State and central New England between 1835 and 1984 is representative of changes in the eastern U.S. (Figure 1), reduced frequency and intensity of drought along with warming could account for a considerable proportion of the increased growth rates. Teasing out the many factors contributing to the increase in growth rates, however, will be difficult considering the potentially interrelated nature of increased warming, precipitation, elevated atmospheric CO_2, and nitrogen deposition.

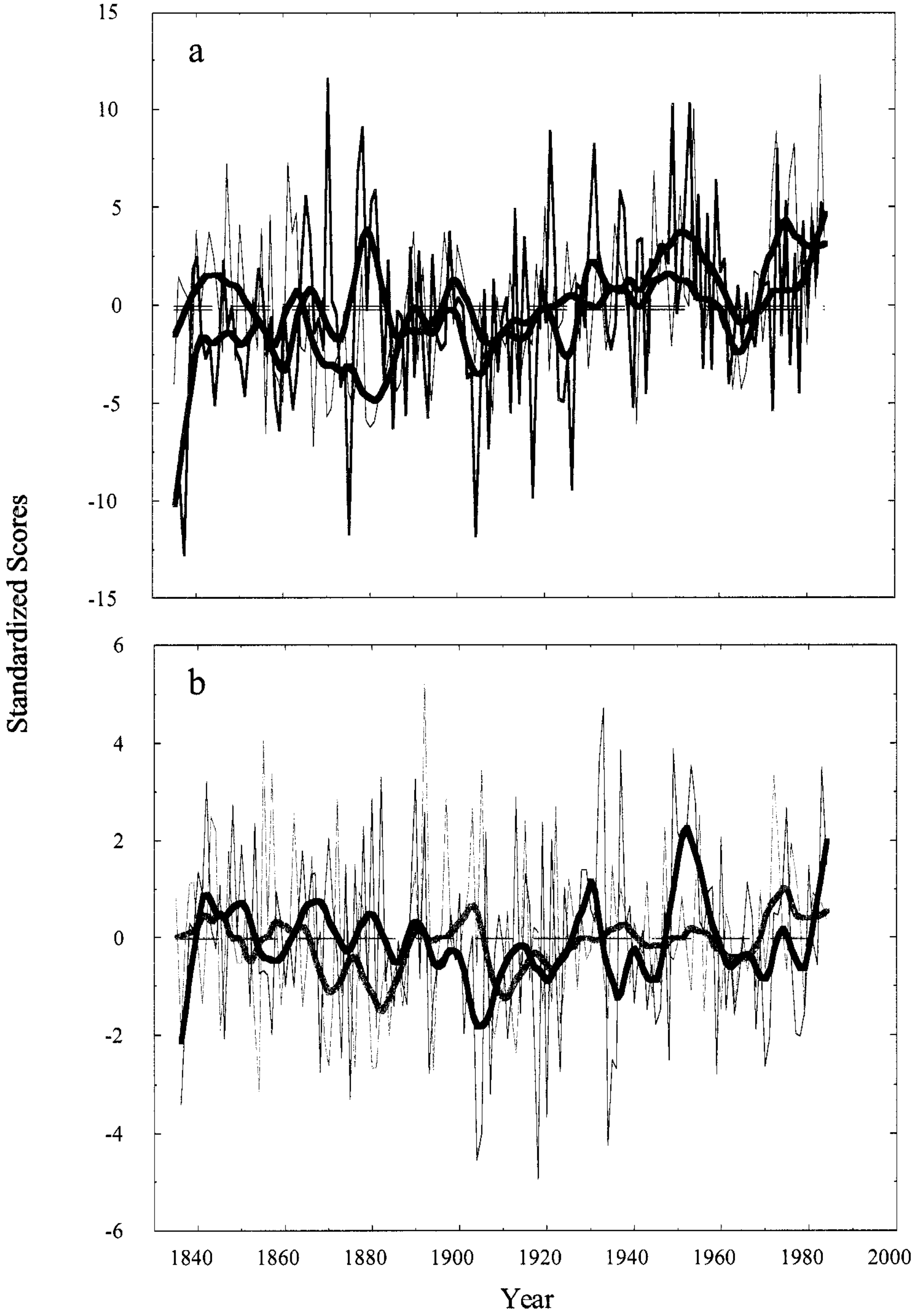

Figure 1 - Standardized a) Annual and b) Seasonal Climate in Northern New England: 1835-1984. a) Total annual precipitation (blue line) and mean annual temperature (red line). b) total summer (Jun., Jul., Aug.) precipitation (gold line) and mean winter (previous Dec., Jan., Feb.) temperatures (blue line). Horizontal dashed lines show mean for each time series (color corresponds to climate variable). Average annual temperature and precipitation has increased between 1835 and 1984. Seasonal climate has had a relatively const and trend for the entire record, although both summer precipitation and winter temperatures have increased since the early-1900s.

Perhaps the most interesting aspect of the results presented here is that age does not limit tree growth rates. This evidence comes from several independent sources. First, most chestnut oak, white oak and yellow-poplar trees greater than 150 years old had accelerated growth rates since the mid-1850s (Chapter 4). Even the oldest-known individuals of each of these species had some of their widest rings at more than 95% their maximum known age. Second, older NRO populations have higher individual growth rates after the influence of site quality is removed (Chapter 3). Third, there is no correlation between age and trend in growth rates of NRO between 1977 and 2001. Finally, the repeated defoliation of old-growth NRO by gypsy moth in 1945-1946 provides another piece of evidence indicating that age is not a primary limiter of tree growth rates. Growth rates of NRO at Wachusett Mountain in the five years following defoliation were greater than the preceding five years (Appendix B) even though average tree age during the recovery was one-half maximum known age. The Wachusett Mountain findings are in agreement with other findings that suggest that other factors influence the recovery following defoliation (Hogg et al., 2002). Combined with results presented here, the emergent pattern from a variety of tree growth and stand level productivity studies is that age is not the limiting factor of tree growth rates (*i.e.,* Marshall, 1927; Assman, 1970; Lamarche et al., 1984; Carey et al, 2001; Latham and Tappeiner, 2002; Mund et al., 2002; Bascietto et al., 2003; Knohl et al., 2003).

Although increased tree growth rates may not translate proportionately to increased stand or ecosystem level productivity (Mund et al., 2002), two lines of evidence indicate that tree growth rates might be representative of increased productivity. First, there are strong relationships among age, living biomass and total ecosystem carbon in temperate forests; older forests tend to have greater amounts of biomass than younger forests (Pregitzer and Euskirchen, 2004). Second, site index, a measure of site productivity based on tree height, has recently been shown to change as growth factors change, especially temperature (*e.g.,* Boyer, 2001; Hökkä and Ojansuu, 2004; Nigh et al., 2004). As climate change can increase tree growth rates, it appears it also increases site productivity and, in turn, carbon sequestration.

Increased productivity in old-growth forests, however, has important implications for forest conservation and management. Declining growth rates, so-called overmaturity, is used as justification for cutting to improve tree and forest productivity and shorter cutting rotations (e.g., Hamilton and Johnson, 1994). Results here show that tree productivity in natural, mix-aged and mix-species forests does not necessarily decline with age. The practical application of these results is that older forests, such as old-growth or old second-growth, could be productive well beyond normal cutting rotations, which would justify management plans with cutting rotations from one to two centuries or more, depending on the species being managed. Also, as it is more difficult in the eastern U.S. to justifying protecting previously-cut forests versus uncut forests, these results would support the conservation of old, second- or third-growth forests for carbon sequestration as they hold the potential for continued productivity.

Elevated CO_2, nitrogen, climate change, land-use history and forest maturation are important factors of the sequestration of atmospheric carbon (*i.e.,* Caspersen et al., 2000; IPCC, 2001; Joos et al., 2002; Mathews et al, 2005). Results presented also show that winter temperatures need to be considered as an important additional factor as well (Pederson, et al., 2004; Chapters 2, 3; Hopton and Pederson, in press; Appendix A).

Large-scale gradients not previously studied, like snow cover, may also play an important role in carbon sequestration (Pederson et al., 2004; Chapter 2). These results underscore the importance to look beyond the one or two variables known to dominate tree growth rates. For example, NRO growth rates in the northeastern U.S. peaked during periods of reduced drought and gypsy moth defoliation and increased winter temperatures. Red maple growth rates may be limited by a complex interaction of climate, gypsy moth defoliation and successional trajectories (Chapter 3). In light of evidence presented here confirming the role of geography in the climatic sensitivity of many tree species and a large amount of evidence contradicting the long-held tenet that tree growth declines with age, it is apparent that there is still much to learn about the long-term interaction between environmental factors of tree growth and the carbon cycle, even in a heavily studied region like the eastern U.S.

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Appendix A: Climate Sensitivity of Atlantic White Cedar at Its Northern Range Limit

Hopton, H.M. and N. Pederson. In press. Climate sensitivity of Atlantic white cedar at Its northern range limit. In: Burke, Marianne, K.; Sheridan, Phillip, eds. 2005. Atlantic white cedar: ecology, restoration, and management: Proceedings of the Arlington Echo symposium. Gen. Tech. Rep. SRS-XX. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: XX-XX.

Note: Paper included with permission from Louise A Wilde for the U.S. Forest Service.

Also, this galley contains two small errors:

Results- Saco Heath (pg. 25)

*2nd column, first line (9th line of paragraph) - table 3 should be table 2

*2nd column, last line (18th line of paragraph) - table 2 should be table 3

CLIMATE SENSITIVITY OF ATLANTIC WHITE CEDAR AT ITS NORTHERN RANGE LIMIT

H. Myvonwynn Hopton and Neil Pederson[1]

Abstract—Atlantic white cedar is a wetland tree species with ecological and commercial importance that is distributed primarily along the Atlantic seaboard to south central Maine. The number of AWC swamps has declined due to human impacts. The potential for rapid climate change and AWC's threatened status make it important to study factors affecting its growth, especially climate. The objectives of this study are to determine the usefulness of AWC for tree-ring analysis, its sensitivity to climate along its northern range limit, and to study its growth rates. Seven AWC populations from northern New Jersey to southern Maine were found to be sensitive to changes in its environment. Growth was most commonly correlated to prior May and June, winter through spring, and current July and August temperatures. Decadal variations in temperature closely mirror variations in AWC growth suggesting that temperature is the primary limiting factor across the region from 1902 to 1995.

Keywords: Climate change, northern range limit, temperature, tree growth, tree productivity.

INTRODUCTION

Atlantic white cedar (AWC), [*Chamaecyparis thyoides* (L.)] ecosystems in the Northeastern United States are deemed threatened because of their rarity in the landscape. New Jersey's AWC population has decreased 74 percent from its estimated historic area (from 47,000 ha down to 12,100 ha) (New Jersey Department of Environmental Protection 2003). In the glaciated Northeast, only 5,300 ha of AWC swamp remain (Motzkin 1991). The primary causes of their net loss over the last two centuries are logging and habitat destruction (Laderman 1989).

Atlantic white cedar is important commercially and has been heavily logged since colonial times because of its workability and resistance to decay and insects. AWC has been historically used for shingles, barrels, and boats. Today it is still an important commercial tree in New Jersey, Virginia, the Carolinas, and Florida, and is often used for telephone poles, piling, ties, and siding (Little and Garrett 1990).

Atlantic white cedar ecosystems are ecologically important because they provide unique cover, habitat, and food for a variety of fauna. For example, a plant survey of a recently discovered AWC community in west central Georgia contributed significantly to the knowledge of rare plant occurrence within the region (Sheridan and Patrick 2003). The larva of the endangered Hessel's Hairstreak butterfly (*Callophrys hesseli* Rawson and Ziegler) feed solely on AWC leaves in Maine (Kluge 1991). White-tailed deer (*Odocoileus virginianus* Boddaert) preferentially eat AWC seedlings as a food source (Dickerson 2002). Therefore, studying, protecting, and managing AWC ecosystems is beneficial both for commercial and ecological reasons.

Atlantic white cedar grows along the Eastern Coast of the United States no more than 130 miles inland, with its northern range limit in south central Maine (Little and Garrett 1990). Because of its economic and ecological value and threatened status as an ecosystem, it is important to understand what factors limit the growth of AWC for future management and conservation. Studying AWC's climatic sensitivity is especially important in the face of potential rapid climate change although the species is not traditionally used in dendrochronological research. Nevertheless, Golet and Lowery (1987) found that changes in measured relative ring width could be explained by variations in water level in several Rhode Island AWC swamps. However, they concluded that their findings were wetland specific without a strong regional climatic signal. Pederson and others (2004) found AWC to be very temperature sensitive in southern New York State and northern New Jersey region. It is not known if this sensitivity can be extended to a regional scale.

The objectives of this study were to: (1) identify how well AWC crossdate (agreement in population's annual radial growth variations), (2) improve our understanding of the climate response of AWC, and (3) study its growth over the last 100 years. Specifically we tested whether the trees along their northern range limit show sensitivity to climate and if so, which climatic variables account for variations in annual ring widths. Although not often tested in temperate regions, it is thought that trees are more sensitive climatically at range limits. Research on loblolly pine (*Pinus taeda* L.) indicates that cool temperatures only became a growth-limiting factor at its northern range limit (Cook and others 1998). Therefore, we hypothesized that radial growth at the northern range limit for AWC was most limited by temperature of the previous and current growing season.

PROCEDURE

Increment cores were collected from seven different sites along the northern edge of Atlantic white cedar range limit:

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Appleton Bog, ME, Saco Heath, ME, Westminster, MA, Monson, MA, North Madison, CT, High Point, NJ, and Uttertown, NJ (fig. 1). To characterize forest composition at each site, four measurements of basal area (BA) using a cruise prism were taken at every fourth or fifth tree cored and averaged. Here we report only those species making up > 10 percent of stand BA (table 1).

Cores were collected and processed using standard dendrochronological techniques (Fritts 1976, Stokes 1968). Dr. Thomas Siccama and his students at Yale University collected cores from North Madison Cedar Swamp, Connecticut in 1988, 1991, and 1992. The cores were loaned to the Lamont-Doherty Tree Ring Lab for this study. Basal area measurements were not available for this site. From each of the other sites, cores were collected from at least 20 different trees using a hand-operated increment borer, except for Monson, MA due to its lack of old trees. Since climate response was the focus of this study, healthy dominant older looking trees were selected for coring so as to maximize the climate response. This non-random selection may not fully represent the stand-level climate response. However, some research suggests that competition can obscure the temperature signal in trees (Cescatti and Piutti 1998). Also, trees in declining health may be unresponsive to climate. Therefore, in keeping with the study's main goal we avoided sampling understory or unhealthy appearing trees. To maximize the geographic coverage while minimizing field and laboratory time, a single core was taken from each tree sampled. A second core was occasionally taken if the tree appeared old to increase sample replication and strengthen the cross-dating. This is less than the typical tree ring protocol of two cores per tree. However, tree replication is more efficient than core replication in reducing estimated mean standard error (Fritts 1976). Once the cores were extracted, they were stored in labeled plastic straws for transport back to the Lamont-Doherty Tree Ring Lab, Palisades, NY.

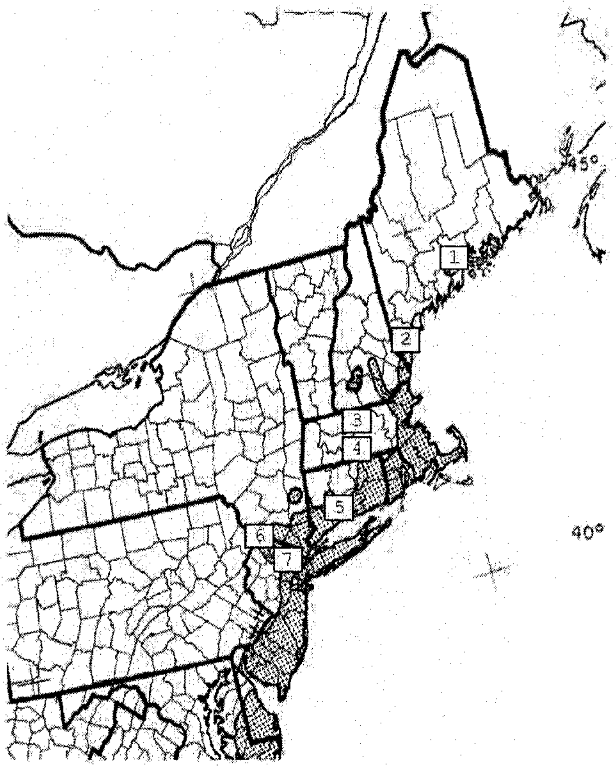

Figure 1—Atlantic white-cedar populations sampled in the Northeastern United States: 1 - Appleton Bog, ME; 2 - Saco Heath, ME; 3 - Westminster, MA; 4 - Monson Cedar Swamp, MA; 5 - North Madison Swamp, CT; 6 - High Point, NJ; 7 - Uttertown Bog, NJ. Stippled area represents the northern distribution of Atlantic white-cedar as adapted from Little (1971).

Table 1—Site information for the Atlantic white cedar stands sampled

Site	County	Latitude/longitude	Elevation	Stand BA (STD)
			m	m^2/ha
Appleton Bog, ME	Knox	N43°33' W70°28'	120	66.0 (15.3)
Saco Heath, ME	York	N44°20' W69°16'	40	35.5 (24.0)
Westminster, MA	Worcester	N42°32' W71°57'	250	47.3 (22.8)
Monson, MA	Hampden	N42°03' W72°18'	260	46.0 (6.9)
Madison, CT	New Haven	N41°21' W72°38'	80	—
High Point, NJ	Sussex	N41°38' W74°39'	460	54.8 (17.9)
Uttertown, NJ	Passaic	N41°10' W74°25'	300	79.2 (15.7)

BA = basal area.

At the lab, the cores were air-dried and then glued to wooden mounts. The cores were sanded with increasingly finer sandpaper up to 600 grit. The cores were then examined under a microscope and visually cross-dated. Rings were measured to the nearest 0.001 mm. Visual cross-dating was verified using the program COFECHA (Holmes 1983). Correctly dated time-series of growth were standardized using a double detrending method with the intent to preserve as much low frequency information as possible unrelated to competition (Cook and Kairiukstis 1990). First, a negative exponential curve or linear regression was used to remove geometric growth trends caused by the narrowing of rings as stem diameter increases. If a step change in growth was observed, a second detrending was done using a two-thirds spline to remove increases in growth related to changes in local competition (Lorimer and Frelich 1989). Standardized ring widths were then averaged to create an index of growth for each site.

Chronology signal strength was characterized using series intercorrelation (SNC) and the between tree expressed population signal (EPS). SNC indicates the strength of the common signal within a sample population and is derived from the correlation between all time-series of growth. EPS is a function of the mean correlation of all growth series within a population and sample size (Wigley and others 1984). It describes how well a finite sample size estimates the infinite, hypothetical population. These statistics are among the most commonly used indicators of agreement in year-to-year growth among trees within a population (Cook and Kairiukstis 1990).

The climatic sensitivity of each population was found by correlating the standardized ring index chronology against mean monthly temperature and total monthly precipitation from prior March to October of the current growth year. We chose a 20-month period of climate for correlation analysis as climate of the prior year can influence ring width of the current year (Fritts 1976). Because long-term meteorological records of minimum and maximum temperatures are lacking in the Appleton Bog region of ME, we chose to use gridded meteorological data from the Climatic Research Unit (CRU) of the University of East Anglia, UK (Jones 1994, New and others 2000). Grid points are located every 0.5 degrees and are interpolated climatic data from the eight nearest stations. For our purposes, data from the grid point closest to the sample site was used. Data is available from 1901 to 1995. Correlations were considered significant at $p \leq 0.05$ unless otherwise stated.

Regional Temperature and Growth Trends

To test if the climate signal in AWC is potentially regional, we compared a time-series of regional temperatures with a time-series of regional growth. Using CRU data, the months of temperature most commonly correlated to growth (prior May and June, prior November though current May and current July and August) were averaged using a mean and variance corrected arithmetic average procedure. This time-series covers 1902 to 1995 because 1 year is lost due to the combination of months from the prior and current years (e.g. May, June, November and December 1901 combined with January to May and July and August 1902). An arithmetic average was made of the standardized chronology of each population to create the regional time-series of growth.

RESULTS

Appleton Bog, ME

Appleton Bog is unique in that it is the northernmost known stand of AWC (Stockwell 1999). The forest floor is covered with *Sphagnum* moss and fern species. AWC dominates the canopy, comprising 77.3 percent of the basal area (BA), with occasional red maple [*Acer rubrum* L. (13.6 percent)] and black spruce [*Picea mariana* Mill. (12.5 percent)] present. Maximum tree age was 141 years with more than one-half of the trees older than 119 years (table 2). The SNC was r = 0.616, which is well above the 99 percent confidence level of 0.328 (Holmes 1983). EPS value for the Appleton Bog chronology was 0.929, which is above the accepted level of 0.85 (Wigley and others 1984). The standardized ring index chronology showed below average growth in the early 1920s and 1960s while above average growth occurred in the mid-1920s through the mid-1950s and from the mid-1970s until the mid-1990s (fig. 2A). Appleton Bog AWC was positively correlated with temperature during the prior May, June, September, November, and current January through April (table 3). These months accounted for 29.6 percent of the ring width variations. Only 3 months show positive correlation with precipitation: prior August, current March and July accounted for 8.80 percent of the growth variation.

Saco Heath, ME

Saco Heath is the only known domed-bog to support AWC (Laderman 1989). Saco Heath is composed of scattered aggregations of trees through out a dense shrub layer dominated by blueberry (*Vaccinium* spp. L.). In the forested areas, AWC is the dominant tree comprising 82.9 percent of the BA, while white pine (*Pinus strobus* L.) is present to a lesser extent at 12.7 percent. Maximum tree age at Saco Heath was 129 years with more than one-half of the trees older than 100 years (table 3). The SNC was $r = 0.567$ while the EPS was 0.933. The ring index chronology had growth trends similar to Appleton Bog. The early 1920s and 1960s were a decade of below average growth (fig. 2A). The low growth in the 1960s was followed by a period of unprecedented above-average growth that lasted to the present. March to August and November to December temperatures of the previous growing season, and January to February and April to August temperatures of the current growing season were positively correlated with growth (table 2) and accounted

Table 2—Statistical characteristics of the final Atlantic white-cedar chronologies[a]

Site	Trees	Cores	Interval	Median age[b]	Rbar	EPS	Number of samples EPS = 0.85	Date when sample depth = 0.85 EPS[c]
	- - - *number* - - -		*years*	*min/max*				
Appleton Bog, ME	21	29	1862 – 2002	119 (63/141)	0.375	0.929	10	1879
Saco Heath, ME	20	30	1874 – 2002	100 (69/129)	0.583	0.933	5	1879
Westminster, MA	26	29	1859 – 2002	111 (82/200)	0.378	0.922	10	1887
Monson, MA	16	17	1865 – 2002	116 (53/138)	0.531	0.926	5	1870
Madison, CT	21	22	1819 – 1992	142 (92/174)	0.608	0.974	4	1831
High Point, NJ	20	31	1807 – 2002	150 (104/196)	0.393	0.936	9	1830
Uttertown, NJ	20	20	1762 – 2002	125 (72/242)	0.257	0.863	17	1897

EPS = expressed population signal.

[a] Rbar is the average correlation between all trees. EPS is the expressed population signal. See text for more details.

[b] Tree ages are likely higher than shown since several sites had some rot, especially Westminster, MA and High Point, NJ.

[c] This column refers to the date when the sample depth equals the number of cores required to reach an EPS value of 0.85 for each chronology. Before this date, sample depth declines and it is expected that the EPS value would drop below 0.85.

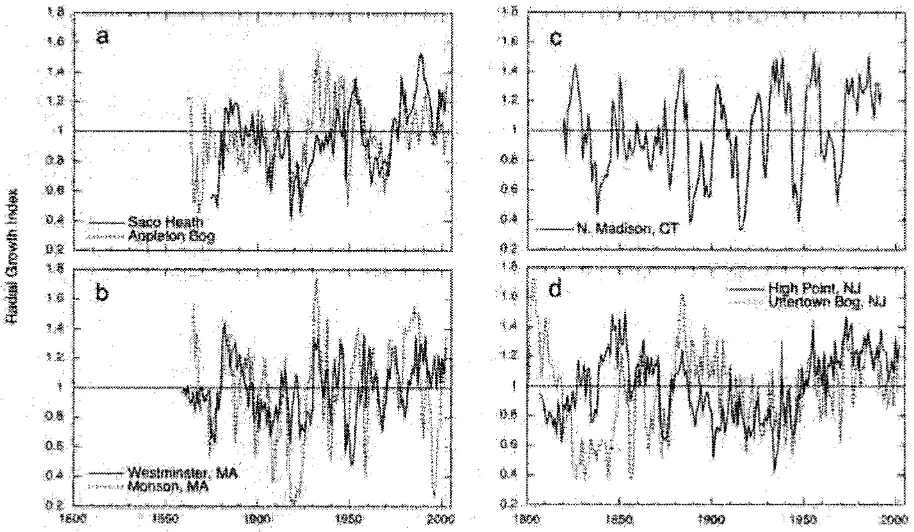

Figure 2—Standardized radial growth chronologies for: (a) Maine (b) Massachusetts (c) Connecticut, and (d) New Jersey. See text for details of each site within each State. Growth is standardized about a dimensionless index of one represented by the horizontal flat line.

Table 3—Significant correlation between Atlantic white cedar growth and mean monthly temperatures

Site	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O
Appleton Bog, ME			**	**			**		*		**	*	*	*						
Saco Heath, ME	**	***	**	*	**	*			**	**	***	***		**	**	*	**	***		
Westminster, MA			**	**			**		**				*		*			*	*	
Monson, MA			**				*		*			*								
Madison, CT			**	**	*					*		*	*	*	*	*	*			
High Point, NJ		*				**			***	*	*	***		**			*	***		
Uttertown, NJ			*							*			**	*						
Number of sites with significant correlation	1	2	6	4	2	2	3	0	5	4	3	5	4	5	3	2	3	3	1	0

* = a significant relation between 0.01< and < 0.05; ** = significance between 0.001< and ≤ 0.01; *** = significance between < 0.001.

for 44.46 percent of the annual growth variation. Growth at Saco Heath was also positively correlated to mean monthly precipitation data for August and November of the previous growing season, and March to April and August of the current growing season. These months accounted for 27.68 percent of the growth variation.

Westminster, MA

The Westminster forest is comprised of AWC (60.3 percent BA), tamarack [*Larix laricina* (Du Roi) K.Koch (38.1 percent)], red maple (16.9 percent), and red spruce [*Picea rubens* Sarg. (14.8 percent)]. Maximum tree age in this population was 200 years with more than one-half of the trees older than 111 years (table 2). The SNC was *r* = 0.565 while the EPS was 0.922. Radial growth was generally below the average value between the 1900s and the mid-1950s (fig. 2B) and above the average value after the 1950s. Growth of the Westminster population was positively correlated to the previous years May to June, September, and November temperatures, as well as current March, May, August, and September temperatures (table 3). Growth was positively correlated with precipitation of the current July and September. Temperature accounted for 30.54 percent of ring width variation, while precipitation accounted for 11.23 percent.

Monson, MA

At Monson, AWC comprises 42.2 percent of the BA, with 26.0 percent red spruce, 25.0 percent eastern hemlock (*Tsuga canadensis* L.), 18.8 percent eastern white pine (*Pinus strobus* L.), and 16.7 percent red maple. Monson has field evidence of logging within the last 70 years. Maximum tree age at Monson was 139 years with more than one-half of the trees older than 116 years (table 2). The SNC was r = 0.622 while the EPS was 0.926. Radial growth was generally below average growth from the 1900s to the mid-1950s (fig. 2B). The radial growth index showed a period of decreasing ring width from the 1890s to the early 1920s. Growth from 1970 through the mid-1980s was above average and has since decreased considerably. Growth in the Monson AWC population was positively correlated to the prior year's March, September, November and current February temperatures (table 3) and accounted for 16.37 percent of the ring width variations. Only a wet prior November was correlated to growth and accounted for 4.02 percent of the annual growth variation.

North Madison Cedar Swamp, CT

The North Madison Cedar Swamp is a late-successional bog-forest dominated by AWC, with scattered red maple (Andrews and Siccama 1995). Maximum tree age in the North Madison Cedar Swamp was 174 years with more than one-half of the trees older than 142 years (table 2). The SNC was r = 0.616 while the EPS was extremely high at 0.974. Radial growth was below average from the 1840s through the early 1920s, after which growth was above average except for a dip in the 1960s (fig. 2C). Growth in the North Madison AWC population was positively correlated to prior May to July and December, and current February to July temperatures (table 3). These months accounted for 19.49 percent of annual growth variations. A wet current October was positively correlated to growth accounting for 5.71 percent variance in ring width.

High Point State Park, NJ

High Point's AWC population is growing at the highest recorded elevation for the species (Laderman 1989). AWC makes up 73.9 percent of the total BA with eastern hemlock (13.7 percent) and red maple (10.9 percent) as the next most dominant trees. Maximum tree age in the High Point was 196 years with more than one-half of the trees older than 150 years (table 2). Several of these trees were hollow, and this prevented analysis of growth in older wood. Hence, age structure is a bit older than what can be reported here. The SNC was *r* = 0.549 while the EPS was 0.936. The standardized chronology shows a decline in ring width from the 1850s until the 1950s, after which ring width was above average (fig. 2D). This population was very sensitive to temperature (table 3), and growth was positively correlated to prior April, August, November, December, and current January, February, April, July and August. Temperature accounted for 37.54 percent of the ring width variation. Only 2 months, May and November of the prior growing year was positively correlated with precipitation and accounted for 11.43 percent of the ring width variation.

Uttertown Bog, NJ

Uttertown Bog is one of New Jersey's few remaining peatlands (Kuo 2003). AWC represents 80.3 percent of the BA, with eastern hemlock representing 18.0 percent. Maximum tree age in Uttertown Bog was 242 years with a majority of the trees between 100 and 140 years old (table 2). The SNC was *r* = 0.566 while the EPS was only 0.863. Radial growth increased from the 1860s until the 1910s, followed by a period of decline until the 1950s (fig. 2D). Following a slight dip in the 1960s, growth has increased since the 1970s. Uttertown was one of the least climate-sensitive populations studied here. Prior April and December and current January and April temperatures were positively and significantly correlated to climate (table 3) accounting for only 10.07 percent of the ring width variation. Prior May and December and current May and June precipitation were significant and positively correlated to growth. Precipitation accounted for 13.88 percent of the variation in ring width.

Regional Temperature and Growth Trends

There was a strong agreement between regional temperature and AWC growth ($r = 0.66$; $p < 0.0001$) from 1902 to 1995 with temperature accounting for 42.9 percent of variation in growth. The agreement is especially evident at decadal time scales (fig. 3).

DISCUSSION

Usefulness of AWC for Dendrochronology

Our results show that AWC growth is very sensitive to environmental conditions, making it useful for tree-ring analysis. The between-tree EPS was high (> 0.920) in six of the seven populations and suggests a strong common signal. Though not the focus of this study, individual trees from several populations showed possible release from competition that was likely related to canopy disturbance. Standard disturbance detection methods may be used to reconstruct stand history using AWC (Lorimer and Frelich 1989).

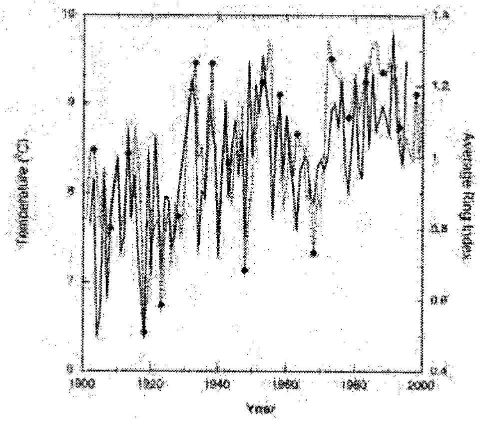

Figure 3—Regional temperatures (solid line) versus regional standardized growth of Atlantic white cedar (dashed line with solid diamond symbols). See text for further details.

The primary limitation for the dendroclimatological use of AWC at the sites studied is its current age structure. Most stands sampled were < 130 years in age. The Uttertown site appears to be essentially an even-aged 120 year-old forest with a few scattered old trees. North Madison, CT and High Point sites had the least disturbed forests of the sites studied and yet no trees older than 200 years were found. If available, sub-fossil or relict wood samples could be analyzed in an attempt to extend stand disturbance history and chronology length. Given AWC's responsiveness to environmental variation, it is likely worth the effort and expense of relict wood recovery. Such a collection would greatly enhance our knowledge of long-term climate variability and AWC ecology in a heavily populated region, which may be useful for restoration of AWC ecosystems.

Climate Response

In general, AWC has a positive correlation to temperature at its northern range limit (fig. 4). Across all sites the monthly temperatures most frequently correlated with growth were prior May and June, prior winter through current spring (November to May), and current July and August temperatures (table 3). The strongest correlations between growth and temperature were during winter months. More than one-half of the sites sampled had levels of temperature sensitivity similar to the trees used for the only Eastern United States temperature reconstruction (Conkey 1982). Temperature accounted for 29.6 percent or more of annual growth variation at four sites making AWC one of the most temperature sensitive trees in the Eastern United States.

Of the sites sampled, correlations were strongest at Saco Heath, Appleton Bog, and Westminster Swamp, indicating that temperature is most important near the northernmost end of AWC's range limit. More southerly populations at North Madison and Uttertown had a lower sensitivity to temperature variation. These results are similar to the temperature

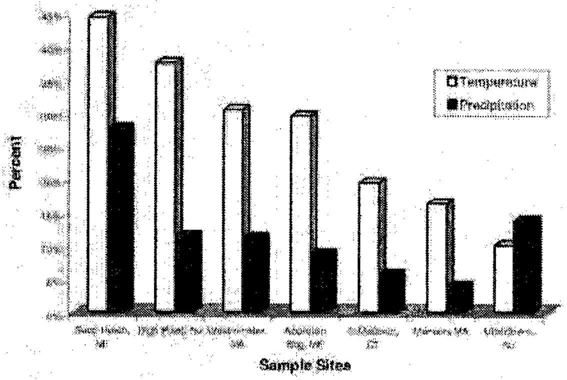

Figure 4—Sites are listed from left to right in the order of decreasing temperature sensitivity. The y-axis represents the amount of annual ring width variation that can be accounted for (r-squared) by temperature (open bars) and precipitation (black bars). See text for further details.

sensitivity for growth documented previously for loblolly pine (Cook and others 1998).

High Point, NJ is an exception to the geographic trend in temperature sensitivity. While High Point was one of the more southern sites sampled, AWC growth was one of the most sensitive to climate, but this population is growing at the highest known elevation for the species and likely experiences lower temperatures than other populations at that latitude. Using the CRU meteorological data, mean annual winter and summer temperatures from 1901 to 1995 for High Point fall close to those for Saco Heath, ME. Average summer and winter temperatures at High Point are 21.06 °C and -1.66 °C, respectively. At Saco Heath summer and winter temperatures averaged 20.06 °C and -3.66 °C. However, there is a significant difference between the elevation of the High Point AWC population (460 m) and the closest meteorological station most likely to have been heavily weighted in the CRU interpolation data (Point Jervis, NY, 143 m). Assuming an average environmental lapse rate of 0.65 °C cooling per 100 m in elevation, the mean summer and winter temperatures at High Point would actually be roughly 19.00 °C and -3.72 °C, respectively. Thus, the temperatures in which the High Point AWC trees live would fall within the range of temperatures of the Maine AWC sites, possibly explaining the exception in the geographic trend.

If AWC responds like other tree species, the reduced temperature sensitivity of populations at more southern sites may be the result of location in the species' range (Cook and others 1998) or greater competition with other plants (Cescatti and Piutti 1998). The current age structure at the Monson site suggests stands are still in the stem exclusion stage during which competition induces self-thinning and excludes tree recruitment (Oliver and Larson 1996). As a result, stand development at Monson may be contributing to AWC's reduced temperature sensitivity at this site.

The Uttertown site was the only site where growth was more sensitive to precipitation than temperature. Also, it was the southernmost site sampled. In addition to a warmer climate than experienced by the more northern populations, increased competition may cause tree growth to be more limited by precipitation as was shown in another tree species by Cescatti and Piutti (1998). While the Uttertown site has the highest estimated BA of the sites sampled, it is similar to the BA of Appleton Bog, near the species' northern range limit. More work is needed to determine if stand densities (a proxy for competition) within one climate region has an influence on AWC's climate sensitivity.

It is interesting to note sites that showed the highest sensitivity to temperature also showed the highest sensitivity to precipitation (fig. 4). The Saco Heath population showed the greatest overall sensitivity to climate. Since Saco Heath is a domed-bog, a unique wetland type for AWC (Laderman 1989), perhaps the site's physical characteristics along with its range position made it the most sensitive to climate. A domed-bog results from the build up of peat over time, which eventually serves to elevate the area from its surroundings so that it is perched above the water table. Surface water does not drain into domed bogs, making precipitation the primary source of water. The physical structure of a domed bog and the resulting hydrological regime would seem to explain Saco Heath's high sensitivity to precipitation. Saco Heath's low stand density (table 1) could also have been a factor in the high temperature sensitivity, following the same logic in the previous paragraph.

Growth Trends

Most sites showed similar decadal variations in growth over the last century, especially over the last 30 years indicating a growth trend for the region (figs. 2 and 3). The recent period of common increased radial growth suggests large-scale influences on growth, such as climate, nitrogen deposition or elevated CO_2. Temperature seems the most plausible explanation for much of the last 100 years. A decline in regional growth trends during the 1960s (fig. 3) in concert with declines in regional and global temperatures (Jones and Moberg 2003) suggest temperature is controlling radial growth. In fact, the CRU meteorological data for our study region and Northern Hemisphere data show that winter and spring temperatures have been rising over the recent decades (Jones and Moberg 2003, Lugina and others 2003) suggesting temperature may be linked to increased radial growth in recent decades.

Minimum temperatures have increased more rapidly than maximum temperatures (Karl and others 1993), which may be an important attributing factor to the increasing growth trend. AWC research of populations in the southern New York State and northern New Jersey region suggests growth is consistently correlated with minimum July and August temperatures (Pederson and others 2004). To date, we don't know if this local sensitivity to growing-season minimum temperature occurs at the regional scale as well.

The Monson site remained the exception to general regional patterns, and had a sharp decline in growth over the last 15 years. The lack of synchronicity in the Monson population may again be attributed to its disturbance history or inadequate sampling for detection of trends.

CONCLUSION

Atlantic white cedar growth is sensitive to changes in its environment. All populations tested showed strong interseries correlation and EPS values, indicating that the trees are responding to a common signal in their environment. More importantly radial growth in AWC at its northern range limit was positively correlated with monthly mean temperature data over the prior and current year. Atlantic white cedar growth also was positively correlated with variations in monthly mean precipitation data, but correlations were not as strong. The sites most sensitive to temperature were also found most sensitive to precipitation.

The forecast of future climatic warming does not appear to pose any immediate threat to growth of this species along its northern range limit. If temperature trends proceed as expected increasing 1.7 to 4.9 °C over the next century (IPCC 2001, Wigley and Raper 2001), growth would likely increase assuming moisture availability does not become a more important limiting factor. This could have implications for future ecosystem management and carbon sequestration modeling. However, how climate change will influence relative competitive ability is unknown.

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Appendix B: Gypsy Moth Defoliation Discussion

Extra Gypsy Moth Defoliation Discussion

There are three unknown decline events in gypsy moth occupied areas (Chapter 4 - Table 11). Growth rates at Mohawk Trail State Forest, MA and Uttertown, NJ recovered to rates of the 5-years prior to each event within fiver years. In contrast, growth rates at Singer Farm did not recover to per-event rates. Latewood characteristics, significant decline in growth rates and limited recovering following the event suggest the occurrence of a gypsy moth event at Singer Farm. Gypsy moth was established in the county in 1979. No one has been able to confirm a gypsy moth event, however, primarily because of the lack of forest in the county (John Lehman, personal communication).

The large network comprised of most trees greater than 100 years old allow the comparison of three strong gypsy moth events, 1945-46, 1981, and 1983(-86) (Chapter Three, Table 11). While not ideal in terms of replication, it is instructive to examine the impacts and recovery of each event. The 1983 event appears to have been the most severe in terms of impact and recovery. A strong recovery occurred following the repeated defoliation in 1945-46 compared to the other defoliations events.

The growth decline event at Uttertown is worth noting. Ring characteristics in NRO and chestnut oak (N. Pederson, unpublished data) strongly suggest a gypsy moth defoliation event. I have not yet confirmed an outbreak in northern NJ during that period. If this decline is a gypsy moth event, the strong recovery following the decline appears to be anomalous compared to previous analyses of gypsy moth defoliation (Campbell and Garlo, 1982; Naidoo and Lechowicz, 1999; Muzika and Liehbold, 1999; Chapter Three).

The 1983 event appears to have been the most severe in terms of impact and recovery. This might be complicated, however, as gypsy moth was new to the western NY region. Growth losses can be less during a second outbreak or there can be a better growth response and faster recovery in trees surviving earlier gypsy moth defoliations (Campbell and Garlo, 1982; Gansner et al., 1993; Naidoo and Lechowicz, 1999). If ecosystems are adapting to gypsy moth (Swain, 1983; Muzika and Liehbold, 1999), ecosystem resiliency in this region could have been low during the 1990-1991 events at Singer Farm.

The strong recovery following the repeated defoliation in 1945-46 would suggest that younger trees have a greater ability for recovery. This hypothesis is not supported, however, by the fact that the Wachusett Mountain old-growth NRO completely recovered five years after the defoliation event. Average tree age at Wachusett Mountain in 1945 was 172 years, which is one-half maximum known age for NRO. This evidence suggests that other factors, such as climate, may play an important role on the impact and recovery of defoliation events (Naidoo and Lechowicz, 1999; Hogg et al., 2002). For example, while years of drought preceded the 1945 and 1981 defoliation events, recovery might have been better following the 1945-46 event than the 1981 event because while 1945 and 1946 were wet years while 1981 was dry (Cook and Krusic, 2004). This evidence suggests that age may not be an important limiter in the rate of recovery following gypsy moth events, although this requires much more study.

Synthesis

Aboveground carbon increment rates were reduced on average 36.3% following a gypsy moth defoliation event, which is within the range of growth losses reported in other studies (Baker, 1941; Campbell and Garlo, 1982; Naidoo and Lechowicz, 1999; Muzika and Liehbold, 1999). Growth losses in this study were not corrected for climatic response of NRO, which could be important, as gypsy moth outbreaks are often associated with drought (Naidoo and Lechowicz, 2001). Another difference between this study and prior studies is that prior studies often studied radial growth increments. It is not known whether raw radial-growth increments or aboveground carbon increments best represent growth impacts of gypsy moth defoliation events.

Evidence here shows that gypsy moth defoliation has the strongest and longest lasting impacts on NRO growth rates across New York State and New England compared to climate or disturbance events with a negative impact on growth rates. Average growth rates over the five years following drought or other similar events are equal to or greater than pre-event growth rates. In contrast, growth rates following gypsy moth events recovered to pre-defoliation growth rates only one-third of the time. Average post-gypsy moth growth rates over the five-year after defoliation were within 10% of pre-event growth rates, however, and is in some agreement with previous studies (Campbell and Garlo, 1982; Naidoo and Lechowicz, 1999; Muzika and Liehbold, 1999). Again, these studies did not remove the influence of stem expansion on the width of radial increments. As tree diameter gets larger, radial increments decline in width even if biomass increment is constant. Disregarding this well-known interaction between tree geometry and radial increment widths more than likely overestimates the impact of gypsy moth defoliation.

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Appendix C: Table of Tree-Ring Collections Between 1999 and 2004

Table 1 – Populations Sampled between 1999 and 2004. [a] - Abbreviations explained in Table 2. [b] - Abbreviations explained in Table 3.

#	Site – Species [a]	# trees	# cores	Lat	Long.	Help[b]
1	Alb. Pine Bush, NY - PIRI	**17**	38	N 42 42.092	W 73 50.345	KV, DF, FB, DY
2	B_Isle, MD - CAGL	15	30	N 38 59.074	W 77 14.539	JH
3	B_Isle, MD - QUST	16	32	N 38 59.356	W 77 14.748	JH
4	Bellvale Mtn, NY CHTH	28	45			KV, KS, AK
5	Bent Creek, NC QUAL	17	21			PB
6	Bent Creek, NC QUPR	22	23			PB
7	Black Rock, NY -PLOC	13	27			EM, DF, LP
8	Blue Ridge, VA - QUAL	12	24	N 37 32.186	W 79 29.693	EM, SB, AC
9	Blue Ridge, VA - QUPR	12	24	N 37 32.757	W 79 27.951	EM, SB, AC
10	Breglia Cliffs, NY - QUPR	23	42	N 42 36.515	W 74 19.089	FB
11	Buena Vista, VA - PIRI	21	36	N 37 44.093	W 79 19.322	-
12	Callaway Gardens, GA - QUPR	20	34	N 32 46.347	W 84 54.392	-
13	Callaway Gardens, GA - QUST	20	35	N 32 46.413	W 84 54.183	-
14	Clintonville, NY - PIRI	20	40	N 44 28.099	W 73 38.247	-
15	Colchester, VT - CAOV	16	24	N 44 33.236	W 73 06.594	PC
16	Colchester, VT - QUAL	18	26	N 44 33.236	W 73 06.594	PC
17	Colchester, VT - QUPR	20	36	N 44 33.441	W 73 06.537	PC
18	Cool Springs, NC - QUST	16	27	N 35 11.350	W 77 05.229	-

#	Site – Species[a]	# trees	# cores	Lat	Long.	Help[b]
19	Curtiss-Gale, NY - LITU	20	33	N 43 17.315	W 76 23.312	SB
20	Dare Co., NC - CHTH	20	30	N 35 44.572	W 75 55.711	SM
21	Dark Hollow, NY - QUAL	16	26	N41.23.692	W 74.6.674	PJK, EC
22	Dismal Swamp, VA - CHTH	20	31	N 36 32.198	W 76 28.064	MH, NC
23	Fiddler's Green, VA - BELE	21	34	N 37 46.252	W 79 14.596	-
24	Fiddler's Green, VA - CAOV	20	32	N 37 46.243	W 79 14.496	-
25	Fiddler's Green, VA - LITU	21	38	N 37 46.166	W 79 14.491	EM, SB, AC
26	Fiddler's Green, VA - MAAC	20	34	N 37 46.121	W 79 14.543	-
27	Fiddler's Green, VA - QURU	20	30	N 37 46.166	W 79 14.491	-
28	Glen Lake Fen, NY - PIRI	20	41	N 43.21262	W 73 41.416	MH
29	Goose Egg, NY - QUAL	20	33	N 43 04.100	W 73 17.400	DF, MH
30	Goose Egg, NY - QUPR	23	37	N 43 03.760	W 73 17.890	DF, MH
31	Greenbrook, NJ - CAGL	**11**	24			EM
32	Greenbrook, NJ - LITU	**15**	31	N 40 55.296	W73 55.782	KV, DF, EM, NS
33	Green Ridge, MD - CAOV	**20**	30	N 39 39.414	W 78 24.032	HK
34	G Green Ridge, MD - PIRI	**22**	37	N 39 39.791	W 78 25.121	HK
35	Hague, NY - QUVE	**20**	36	N 43 41.064	W 73 36.148	SB, TN

#	**Site – Species** [a]	**# trees**	**# cores**	**Lat**	**Long.**	**Help**[b]
36	Heart's Content, PA - MAAC	**18**	32	N 41 41.414	W 79 14.818	NB
37	High Point, NJ - CHTH	**21**	41	N 41 19.898	W 74 39.474	MH, ND
38	Hunter Island, NYC - QUST	**16**	29	N 40 52.347	W 73 47.076	-
39	Irish Creek, VA - QUAL	**16**	27	N 37 40.528	W 79 17.282	EM, SB, AC
40	Irish Creek , VA - QUPR	**17**	30	N 37 40.492	W 79 17.048	EM, SB, AC
41	Lil' Scaly, NC - QUAL	20	34	N 35 01.894	W 83 15.476	MH, NC
42	Lisha Kill, NY - BELE	16	27	N 42 47.488	W 73 51.513	DFu
43	Lisha Kill, NY - CAGL	15	25	N 42 47.698	W 73 51.603	DFu
44	Lisha Kill, NY - QUAL	20	25	N 42 47.488	W 73 51.513	EM
45	Mashomack Island, NY - QUST	20	32	N 41 02.490	W 72 17.072	EC, NB
46	Mohonk Preserve, NY - BELE	17	27	N 41 47.918	W 74 06.753	KV
47	Mohonk Preserve, NY - CAGL	20	30	N 41 48.072	W 74 06.341	-
48	Mohonk Preserve, NY - CAOV	1	1			-
49	Mohonk Preserve, NY - LITU	20	36	N 41 48.600	W 74 05.943	KV
50	Mohonk Preserve, NY - PIRI	15	30	N 41 44.278	W 74 12.283	JB
51	Mohonk Preserve, NY - QUPR	20	34	N 41 45.828	W 74 07.479	-
52	Mohonk Preserve, NY - QUVE	20	26	N 41 47.378	W 74 07.537	-

#	Site – Species [a]	# trees	# cores	Lat	Long.	Help[b]
53	Montgoemry Place, NY - LITU	20	32	N 42 00.528	W 73 55.125	AC, KR, DJ
54	Montgoemry Place, NY - QUPR	21	34	N 42 00.682	W 73 55.244	AC, KR, DJ
55	Mt. A., ME - QUPR	20	34	N 43 13.683	W 70 41.352	TZ
56	Mt. Pleasant, VA - CAGL	20	30	N 37 44.103	W 79 13.438	-
57	Mt. Pleasant, VA - QUVE	20	32	N 37 43.846	W 79 13.433	-
58	Nanticoke, MD - CHTH	20	34	N 38 29.103	W 75 47.465	-
59	Noblewood, NY - BELE	20	30	N 44 21.122	W 73 21.693	-
60	Old Maids Woods, NY - QUVE	20	26			-
61	Otter Creek, PA - BELE	20	31	N 39 52.642	W 76 23.237	-
62	Otter Creek, PA - LITU	20	30	N 39 52.708	W 76 23.182	-
63	Otter Creek, PA - QUAL	21	32	N 39 53.000	W 76 23.385	KV
64	Otter Creek, PA - QUPR	29	40	N 39 52.690	W 76 23.274	-
65	Otter Creek, PA - QURU	**20**	30	N 39 52.708	W 76 23.182	-
66	Otter Creek, PA - QUVE	20	32	N 39 52.862	W 76 23.444	KV
67	Pine Barrens upland, NJ - PIRI	20	41	N 39 44.236	W 74 36.776	JR, EW
68	Pine Barrens wet, NJ - PIRI	18	38	N 39 44.283	W 74 36.670	JR, EW
69	Potomac River, VA - QUPR	20	34	N 39 3.487	W 77 19.795	KV, DiP
70	Prospect Mtn., NY - BELE	15	28	N 43 25.050	W 73 43.740	EM, DF
71	Prospect Mtn., NY - CAOV	**23**	41	N 43 25.300	W 73 34.200	EM, DF, BN

#	Site – Species [a]	# trees	# cores	Lat	Long.	Help[b]
72	Prospect Mtn., NY - QUAL	**28**	43	N 43 25.300	W 73 34.200	EM, DF, BN
73	Savage Mtn., MD - QUAL	**20**	34	N 39 31.015	W 79 07.577	MH, BH, NC, NB
74	Savage Mtn., MD -QUPR trail	**18**	30	N 39 30.801	W 79 06.955	MH, BH, NC, NB
75	Savage Mtn., MD - QUPR ridge	**14**	25	N 39 32.078	W 79 06.855	MH, BH, NC, NB
76	Savage River, MD - MAAC	**18**	31	N 39 30.307	W 79 08.580	-
77	Sterling Forest, NY - CHTH	**31**	43	N 41 11.160	W 74 16.83	FF, ND, DF, JSK
78	Stott Farm, NY - CAGL	21	25	N 43 11.280	W 73 29.930	MH
79	Stott Farm, NY - LITU	11	11	N 43 11.280	W 73 29.930	MH
80	Uttertown Bog, NJ - CHTH	21	22	N 41 06.925	W 74 25.201	LL, MH
81	Uttertown, NJ - LITU	20	27	N 41 06.850	W 74 25.199	KV, SI, JC
82	Uttertown, NJ - QUPR	31	57	N 41 06.942	W 74 25.004	MH, EC
	Northern Red Oak-Red Maple/Carbon Network					
83	Aquidneck, RI - QURU	20	40	N 41 34.157	W 71 17.042	TZ
84	Arnot Forest, NY - QURU	20	40	N 42 16.297	W 76 37.606	EM
85	B. Rock Forest, NY I – QURU	30	90			TZ, ND, EM
86	B. Rock Forest, NY II – QURU	30	90			TZ
87	Catskill Mtns., NY A - ACRU	20	40			Paul Sheppard
88	Catskill Mtns., NY B - ACRU	20	40			Charlie Canham
89	Curtiss-Gale, NY – QURU	21	42	N 43 17.315	W 76 23.312	SB
90	Goodnow Mtn., NY - QURU	20	40	N 43 54.463	W 74 13.082	-

#	Site – Species [a]	# trees	# cores	Lat	Long.	Help[b]
91	Goose Egg Ridge, NY - QURU	21	36	N 43 04.100	W 73 17.400	DF, MH
92	Harvard Forest, MA Lyford - ACRU	**35**	105	N 42 31.788	W 72 10.979	TZ, EHP, DB
93	Harvard Forest, MA Lyford - QURU	**35**	105	N 42 31.788	W 72 10.979	GC, EHP, AR, DB
94	Harvard Forest, MA Tower - QURU	**35**	105	N 42 32.202	W 72 10.440	GC, EHP, AR, DB
95	Harvard Forest, MA Tower - ACRU	**35**	105	N 42 32.202	W 72 10.440	TZ, EHP, DB
96	Montgomery Place, NY - QURU	20	40	N 42 00.682	W 73 55.244	AC, KR, DJ
97	Mohawk Trail State Forest, MA - QURU	20	40	N 42 03.654	W 72 18.054	BL
98	Pine Lake, NT - QURU	20	40	N 42 28.280	W 74 55.549	-
99	Prospect Mtn., NY - QURU	**23**	33	N 43 25.096	W 73 45.305	EM, DF, MH, BN
100	Rooster Hill, NY - QURU	**22**	43	N 43 13.818	W 74 31.549	
101	Sheridan Mtn. VT - QURU	**21**	42	N 44 31.704	W 71 38.283	SB, SS
102	Singer Farm, NNY - QURU	**20**	41	N 43 20.978	W 78 39.674	EM
103	Uttertown, NJ - QURU	20	41	N 41 07.024	W 74 25.019	EM
104	Wachusett Mtn., MA - QURU	39	40			DO
105	Warren-Cutler Res., NY – QURU	20	40	N 42 40.947	W 77 25.798	EM, BG, RW
106	Zoar Valley, NY - QURU	20	40	N 42 25.382	W 78 53.670	EM
	Boreal Species					
107	Bellvale Mtn., NY - PIRU	15	31			EM

#	Site – Species[a]	# trees	# cores	Lat	Long.	Help[b]
108	High Point, NJ - PIRU	**20**	41	N 41 19.898	W 74 39.474	CF
109	Lincoln Mtn., NY - PIRU	**21**	44			DF
110	Piseco, NY - BEAL	20	35	N 43 19.632	W 74 38.748	-
111	Piseco, NY – PIRU	20	40	N 43 19.603	W 74 38.600	-
112	Ramshead-Sanctuary, NY - THOC	20	40	N 44 47.065	W 73 22.102	-
113	RamsHorn-Sanctuary, NY - QUBI	**18**	39			DP, KV
114	Raquette Lake, NY - PIRE	**20**	38	N 43 48.380	W 74 36.573	-
115	Shushan, NY - PIGL	**60**	120	N 43 03.440	W 73 21.110	BN, DP, MH, DF
116	Uttertown Bog, NJ - LALA	11	23	N 41 06.925	W 74 25.201	LL
	Black Tupelo Collection					
117	Bear Swmp, NJ - NYSY	21	39	N 39 17.653	W 75 08.003	DA, MA
118	Colchester Bog, VT - NYSY	13	28	N 44 32.649	W 73 17.030	
119	Fiddler's Green, VA - NYSY	14	30	N 37 46.143	W 79 19.340	-
120	Lincoln Mtn., NY - NYSY	**30**	73	N 43 10.480	W 73 49.010	MH, DF
121	RamsHorn NYSY	12	23			DP, DF, KV

Table 2 – List of species acronyms listed in Table 1.

	Abbreviation	Scientific Name	Common Name
1	ACRU	*Acer rubrum*	Red maple
2	BEAL	*Betula alleghaniensis*	Yellow birch
3	BELE	*B. lenta*	Sweet birch
4	CHTH	*Chameacyparis thyoides*	Atlantic white-cedar
5	CAGL	*Carya glabra*	Pignut hickory
6	CAOV	*Carya ovata*	Shagbark hickory
7	LALA	*Larix larcina*	Eastern tamarack
8	LITU	*Liriodendron tulipifera*	Yellow-poplar
9	MAAC	*Magnolia accuminata*	cucumbertree
10	NYSY	*Nyssa sylvatica*	Black tupelo
11	PIGL	*Picea glauca*	White spruce
12	PIRE	*Pinus resinosa*	Red pine
13	PIRI	*P. rigida*	Pitch pine
14	PIRU	*P. rubens*	Red spruce
15	PLOC	*Platanus occidentalis*	American sycamore
16	QUAL	*Quercus alba*	White oak
17	QUBI	*Q. bicolor*	Swamp white oak
18	QUPR	*Q. prinus*	Chestnut oak
19	QURU	*Q. rubra*	Northern red oak
20	QUST	*Q. stellata*	Post oak
21	QUVE	*Q. velutina*	Black oak
22	THOC	*Thuja occidentalis*	Northern white-cedar

Table 3 – List of volunteers who cored trees between 1999 and 2004.

	Name abbreviations	Full Name	Institution
1	DA	Dylan Abrams	Elementary school
2	MA	Marc Abrams	Penn State
3	SA	Susan Ask	Maine TNC
4	BH	Brian Avers	NYU
5	NB	Ned Barnard	Author
6	FB	Fred Breglia	Landis Arboretum
7	DB	David Bryant	Harvard U.
8	DJ	Dorji	Bhutan
9	BB	Brendan Buckley	TRL
10	JB	Jinbao	TRL
11	SB	Sanaa Byambasuren	N. Univ. Mongolia
12	JC	Julie Carson	Cola U
13	EC	Ed Cook	TRL
14	NC	Nic Cook	Albany U.
15	PC	Peter Cottrell	IBM
16	AC	Ashley Curtis	TRL
17	ND	Nicole Davi	TRL

	Name abbreviations	Full Name	Institution
18	CF	Christa Farmer	Cola U
19	FF	Francesco Fiondella	Wall Street Journal
20	DF	Dave Frank	TRL
21	DFu	Dave Furman	TNC
22	BG	Bruce Gilman	FLCC
23	JH	Jane & Bill Hill	Author - Retired
24	MH	Myvonwynn Hopton	Cola U
25	SI	Sarah Ingram	LDEO
26	GJ	Gordon Jacoby	TRL
27	HK	Harry Kahler	MD DNR
28	PJK	Paul Krusic	TRL
29	AK	Alex Kurnicki	Landscaper
30	JSK	John Kush	Auburn U.
31	BL	Bob Leverett	Mathematician
32	LL	Les Lynn	Bergen Co. CC
33	EM	Erika Mashig	TRL
34	SM	Shana Merry	Christopher Newport U.
35	BN	Baatarbileg Nachin	Nat. U of Mongolia
36	TN	Tad Norton	NYS DEC
37	DO	Dave Orwig	Harvard Forest
38	DP	Dee Pederson	Cola. U.
39	DiP	Dick Phipps	Retired
40	LP	Linda Pistolesi	LDEO
41	EP	Elizabeth Hammond-Pyle	Harvard U.
42	KR	Kevin "Kid Rock"	TRL
43	JR	John Romano	Cola. U.
44	AR	Amy Rice	Harvard U.
45	KS	Kirsten Sauer	Cola. U.
46	SS	Steve Slayton	VT State Forester
47	NS	Nancy Slowik	Greenbrook Sanctuary
48	MV	J. Morgan Varner	U of Florida
49	KV	Kevin Vranes	Cola. U.
50	RW	Rob Wink	FLCC
51	EW	Ed Wright	LDEO/TRL
52	DY	David Yarrow	Activist
53	TZ	Tiferet Zimmerman-Kahan	Barnard