RESEARCH ARTICLE

Changing Climate,
Atmospheric
Composition,
and Radial Tree
Growth in a SpruceFir Ecosystem
on Grandfather
Mountain, North
Carolina

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ABSTRACT: Grandfather Mountain (GFM) in western North Carolina has been an International Biosphere Reserve since 1992 and is recognized for its natural beauty and ecological diversity. Sixteen unique ecosystems occur on GFM, including a high elevation forest dominated by red spruce (Picea rubens Sarg.) and Fraser fir [Abies Fraseri (Pursh) Poir]. Changing climatic and atmospheric conditions, especially acidic deposition, can harm spruce-fir forests, and heavily impacted ecosystems can be found in nearby locales (e.g., Mount Mitchell, North Carolina) in the southern Appalachian Mountains. Given the ecological significance of the spruce-fir ecosystem on GFM, the primary objectives of this study were to determine: (1) whether radial growth rates of red spruce have changed in recent decades in response to environmental or climatic stimuli; (2) the driving forces behind radial tree growth; and (3) the degree of climate change experienced on GFM. I sampled 47 red spruce trees and developed a tree-ring chronology using standard dendroecological techniques. I examined the relationships between radial growth, climate variables, atmospheric composition variables, and time using simple correlation and regression. Radial growth rates of red spruce increased through time, and growth rates were sigmificantly related to temperature (positively), days with precipitation (negatively), atmospheric carbon dioxide (positively), and emissions of sulfur dioxides and nitrogen oxides (negatively). In addition, significant climate changes on GFM are evident, with the most dramatic change being an increase in mean summer temperatures in excess of 1.4 °C since 1956.

Index terms: acidic deposition, climate change, Grandfather Mountain, radial growth, red spruce

INTRODUCTION

With such notable historic visitors as John Muir, Asa Gray, and André Michaux, Grandfather Mountain (GFM) in western North Carolina (Figure 1) has long been recognized for its scenic attributes and ecological significance. GFM, an International Biosphere Reserve since 1992, supports a suite of unique ecosystems that occur along an elevational gradient. This outstanding ecological diversity attracts scientists to GFM, but is something even visitors to the mountain appreciate as they transition from a mixed hardwood forest at the base of the mountain (the typical mature vegetation of the North Carolina high country) to a spruce-fir forest, more typical of northerly latitudes, at its peak. The ecosystems that GFM supports, like other high-elevation areas in the eastern United States, are subject to environmental stresses from human activities, such as acid deposition. Additionally, changing atmospheric composition and climate change may serve as drivers of ecosystem change.

Many high elevation spruce-fir forests in eastern North America declined in vigor and health during the 20th century, and acidic deposition is one potential culprit of forest decline (Bruck 1989; Pitelka and Raynal 1989). In short, sulfur dioxides (SO₂) and nitrogen oxides (NO_X) emitted during fossil fuel combustion undergo chemical transformations in the atmosphere

and are deposited, via rainfall, clouds, and dry deposition, in a more acidic form (e.g., as sulfuric and nitric acids) (EC 2010). As the acids work their way through the soil, they both leach out important plant nutrients and inhibit the uptake of nutrients by plants (EC 2010). In turn, trees experiencing acidic deposition are nutrient-stressed and become more susceptible to other stressors that are a normal component of their ecosystem (e.g., extreme cold, insect infestations, drought; EC 2010). On GFM, pH measurements from melted rime ice taken from 1993 to 2007 have ranged from 2.6 to 4.7 (Jesse Pope, Naturalist, GFM, pers. comm. 2008), indicating that a mild-to-severe acidic environment has existed since at least the early 1990s. The pH values recorded on GFM are within the range reported by Anderson et al. (1999) for other high elevation sites in the southern Appalachian Mountains.

At neighboring Mount Mitchell, North Carolina, high elevation conifers experienced dramatic mortality rates in the 20th century (Bruck and Robarge 1988; Little 1997; Silver 2003). Despite evidence that acidic deposition can injure spruce-fir forests (McLaughlin et al. 1987; Arp and Manasc 1988; Driscoll et al. 2001), specific biotic responses are inconsistent, especially at a regional scale. For example, there is no evidence of growth decline in spruce-fir forests on either Mount Mitchell or Mount Rogers in Virginia, both neighbor-

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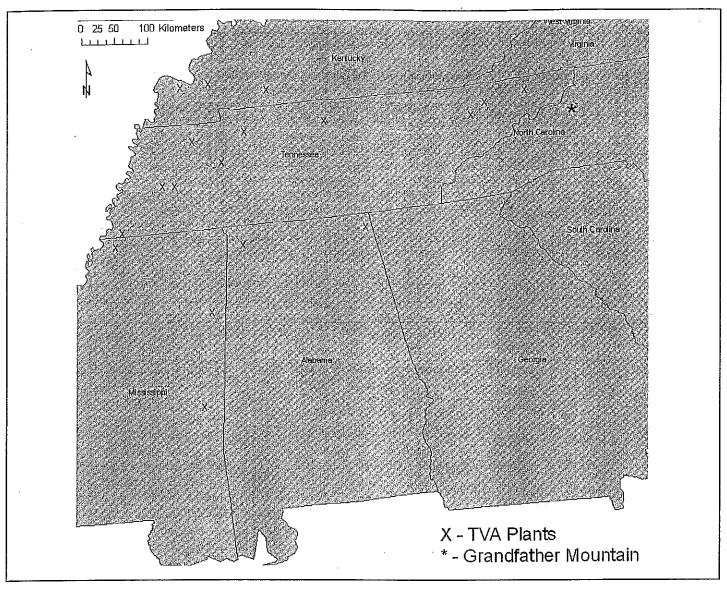


Figure 1. Location of Grandfather Mountain, North Carolina, and Tennessee Valley Authority (TVA) coal or oil-fired power plants.

ing high elevation peaks to GFM (Goelz et al. 1999). Busing (2004) found that red spruce (Picea rubens Sarg.) in the Great Smoky Mountains National Park continued to "grow vigorously" over the period 1993 to 2003 despite an increased mortality rate over the same period, which was attributed to wind or ice storm damages. Adams et al. (1985) and Stephenson and Adams (1995) reported declining radial growth for red spruce in the southern Appalachian Mountains from the 1920s through the early 1980s. While LeBlanc et al. (1992) did find growth declines in 25% of trees from a large post-1967 sample (> 260 trees), especially at elevations above 1980

m, they concluded that "growth decline in red spruce populations from the southern Appalachians is not greater than historical levels for this species and region."

Other aspects of changing atmospheric conditions, including ozone (O_3) , carbon dioxide (CO_2) , and increasing temperature may impact high elevation spruce-fir ecosystems. For red spruce, Rebbeck et al. (1993) reported large (up to 40%) drops in net photosynthesis for trees exposed to high O_3 concentrations. Others (e.g., Thornton et al. 1994; Laurence et al. 1997), however, found no meaningful detrimental effects related to elevated ozone levels. Spruce-fir

forests only exist in the highest elevations in the southern Appalachian Mountains because they are temperature sensitive, generally growing with mean January and July temperatures < -1 °C and 27 °C, respectively (Burns and Honkala 1990). Thus, ecosystem changes may manifest elevationally with continued warming (Kullman 2001), and this could lead to a contraction of the spruce-fir forests on GFM. Alternatively, increasing amounts of atmospheric CO2 could potentially work in an opposite fashion by promoting enhanced growth of coniferous trees (Mooney et al. 1991; Drake and Gonzalez-Meler 1997; DeLucia et al. 1999) and offsetting some

of the negative effects from atmospheric pollutants such as O₃ (Volin et al. 1998). Given the ecological significance of the spruce-fir ecosystem on GFM, the primary objectives of this study were to determine: (1) whether growth rates of high elevation conifers growing on GFM have changed in recent decades in response to environmental or climatic stimuli; (2) the driving forces behind radial tree growth; and (3) the degree of climate change experienced on GFM.

METHODS

Study Area

GFM, located in Avery County, North Carolina, is one of the most prominent peaks within the Appalachian Mountain Range. Known as "Tanawha" by the Cherokee, the name "Grandfather" comes from the profile of the mountain, which resembles an elderly bearded man. Geologically, GFM was formed some 730 million years ago during the Cambrian Period and has subsequently eroded to its current peak elevation of 1812 meters. Although not subject to direct physical alteration from glaciers during the Pleistocene epoch, the climate of that era was influential in the southward migration of various species now endemic to more northerly latitudes. As the Pleistocene ice receded northward, most northern endemic species followed. However, the high elevations of GFM provided a climatic regime well-suited to these species, and they remain today. Owing to its elevational change, GFM now supports some 16 distinct ecological communities and 73 rare species, including the high elevation spruce/fir forests that are the focus of this study (Tager 1999; see http://www.grandfather.com).

Although GFM operated as a private, forprofit scenic attraction from 1952 – 2009, the owners of GFM always maintained a high level of environmental stewardship (see http://www.grandfather.com). To help continue the legacy of GFM as a wildlife sanctuary and nature preserve, Grandfather Mountain State Park was established in 2009 by the North Carolina General Assembly. In addition to the private landholdings of GFM (now managed by the non-profit Grandfather Mountain Stewardship Foundation), 1030 hectares of GFM comprise the state park, and this combines with approximately 1619 hectares of protected conservation easements held by The Conservation Fund and The Nature Conservancy (see http://www.ncparks.gov/Visit/parks/grmo/main.php).

Tree-Ring and Climate Data

I sampled within a 5 km² area of the high elevation red spruce and Fraser fir [Abies Fraseri (Pursh) Poir] ecosystem on GFM, exclusively selecting live red spruce on multiple occasions between June 2006 and March 2008 for dendroecological analysis. The trees were largely distributed near the Grandfather and Underwood trails, which extend from the Mile High Swinging Bridge northeastward to the highest point on the mountain, Calloway Peak (1812 m) (see http://www.grandfather. com/pdf/07trail_map.pdf>). I sampled trees distributed from 36.09 to 36.11°N and 81.82 to 81.84° W, on all aspects, at elevations from 1340 to 1784 m, and predominately on steep slopes (> 25°) within closed-canopy forests. I sampled 47 trees, taking a minimum of two samples from each tree using an increment borer and by following dendroecological techniques (Phipps 1985). For each sampled tree, I recorded its location using a hand-held GPS and noted its general physical attributes (e.g., flagging, crown vigor, presence of dead limbs).

After drying each core in the laboratory, I glued the samples into wooden strips and then sanded them with 320 to 600 grit sandpaper to reveal tree-rings. I cross-dated each sample using standard techniques to determine the precise calendar year of each annual ring (Phipps 1985; Yamaguchi 1991; Stokes and Smiley 1996). I used diagnostic procedures within the computer program COFECHA (Holmes 1983) to confirm the accuracy of the dating after measuring ring widths to 0.001 mm accuracy using a Velmex 24" Unislide, Accu-rite linear encoder, and Quickcheck Digital Readout (Velmex Inc., Bloomfield, New York). For chronology development,

I used the program ARSTAN (Cook and Holmes 1997) and negative exponential or negative linear curve-fitting techniques. The final tree-ring chronology I developed represents the standardized rate of radial tree growth across the site for each year of the data.

I obtained climate data from the National Climatic Data Center's (NCDC) Summary of the Month (NCDC 2008a) for GFM and the closest (8 km) comparable station climatically and elevationally to GFM (1615 m), Banner Elk, North Carolina (1149 m). The GFM station has operated at the same location since 1955, and complete monthly data became available in 1956. As my tree-ring record ended in 2007, I used the period 1956 to 2007 to examine both climatic changes on GFM and the relationships between radial growth rates of trees and climatic conditions. The variables I obtained (all monthly averages or totals) and examined from NCDC were: (1) minimum temperature; (2) maximum temperature; (3) mean temperature; (4) base (18.3 °C) Heating Degree Days (HDD); (5) precipitation; (6) days with precipitation > 0.254 cm; and (7) total snowfall. In addition, I obtained data directly from GFM (Landis Wofford, News Director, GFM, pers. comm. 2008) for days with precipitation (any recorded precipitation). For precipitation, snowfall, and HDD, I used the NCDC data without further modification. Thus, if a month was recorded as having missing data, it was excluded from the analysis. The percentages of months with missing data were 1.4, 0.2, and 3.5 for HDD, precipitation, and snowfall, respectively. For the days with precipitation, I excluded any month (2.4% of total excluded) identified by NCDC as having missing data using NCDC's Cooperative Summary of the Day Inventory Holdings (NCDC 2008b) and any month when NCDC identified more than three days of missing data. For temperature, I used the data from the neighboring station of Banner Elk to replace missing data. In these instances, I established the relationship between monthly values of minimum, maximum, and mean temperature between the GFM and Banner Elk stations using simple correlation. All of the relationships between monthly Banner Elk and GFM data were significant (P <

0.01), with Pearson r-values ranging from a low of 0.58 for September maximum temperature to a high of 0.98 for January mean temperature. I then determined the differences in temperature between Banner Elk and GFM based on monthly averages, and used these averages to adjust the Banner Elk data so that they more accurately reflected conditions on GFM. For example, on average, mean temperatures in January at Banner Elk are 2.2 °C warmer than those recorded on GFM. When I replaced any missing January mean temperature values for GFM with Banner Elk data, the monthly temperature recorded would have been decreased by this amount. If data were identified as missing for any month, or if any days in the month were missing for GFM, I replaced the monthly value with the adjusted Banner Elk data if the Banner Elk data were complete for that month. If any month for GFM had one or two missing days and Banner Elk data were not available, I used the monthly average. If three or more days had missing data, I excluded the month from the analyses. For mean and maximum temperature, 1.44% of months had missing data; and for minimum temperature, 1.76% of months had missing data.

I developed a time series of CO₂ data from two sources. Most of the data (1959 to 2007) were from the NOAA ESRL dataset (see <ftp://ftp.cmdl.noaa.gov/ccg/co2/trends/co2_annmean_mlo.txt>) and represent annual mean values. For 1956, 1957, and 1958, I used the Etheridge et al. (1998) data set derived from East Antarctica ice cores to estimate annual values.

To help determine possible impacts of acidic deposition on tree growth on GFM, I obtained data on sulfur dioxide (SO₂) and nitrous oxide (NO_X) emissions from the Tennessee Value Authority (TVA) (see http://www.tva.com/environment/air/ totaldata.htm>). These data were available for the period 1974 to 2007. TVA is one of the primary sources of atmospheric pollution affecting GFM, operating 18 coal or oil-fired power plants in Tennessee, Alabama, Mississippi, and Kentucky (i.e., states generally upwind of GFM; Figure 1) (see http://www.tva.gov/).

Tree Growth/Climate Modeling and Trend Analysis

I matched the 52 years of available climate data for GFM with the last 52 years of the tree-ring chronology and searched for possible significant growth/climate relationships (P < 0.05) using Pearson correlation. I examined all monthly relationships, including lagged relationships up to one year. I also created a suite of annual (e.g., prior October to current year September), seasonal (e.g., mean June, July, August temperatures), and multi-month (e.g, total precipitation from January to June) variables from the monthly means and totals. After identifying all significant bivariate relationships between radial growth and the climate variables, I created a series of multivariate regression models using all combinations of climate variables that were logically related to radial growth and that did not display high levels of multicollinearity (based on SPSS diagnostics, e.g., VIF). I repeated the process using the two emissions variables (SO₂ and NO_X) in concert with the climate variables and with a total emissions variable which was the base 10 log of $SO_2 + NO_X$. I examined both the radial growth data for the GFM chronology and the large suite of climate variables for significant (P < 0.05) linear relationships over the 1956 to 2007 time period using Pearson correlation.

RESULTS

Growth and Climate/Atmospheric Relationships

The GFM chronology contained 32 core samples with a master series extending from 1858 to 2007 and a sample depth of > 3 cores beginning in 1880. The series intercorrelation was 0.507 and the average mean sensitivity was 0.242. COFECHA flagged six segments with possible problems. I visually rechecked the cross-dating for each core with a flagged segment and determined that those cores were properly dated. The temporal pattern of radial growth for the full chronology shows an extended period of below-normal growth in the late 19th to early 20th century and a trend toward exceptionally above-average

growth during the last decade (Figure 2). Over the time period for which climate data are available for GFM (1956 to 2007), the pattern is one of generally decreasing growth until the early 1980s, followed by sharply increasing growth through 2007.

One of the driving forces for radial growth of red spruce on GFM is temperature (Table 1), with the strongest and most consistent responses occurring for minimum temperatures averaged from the end of the prior year's growing season through the bulk of the current year's growing season. Similarly, HDD, which are a good measure of cumulative temperature stress, relate to radial growth. HDD accumulate daily when mean temperatures fall below 18.3 °C (i.e., a daily mean temperature of 18.3 °C results in 5 HDD). When tallied over a season, year, or multi-month period, low (high) HDD totals represent an extended period with milder (colder) temperatures. In all cases, the temperature or temperature-based variables suggest that radial growth responds positively to warmer conditions. The cumulative number of days with precipitation from the end of the prior year's growing season through the bulk of the current year's growing season is also a driving force for radial growth roughly equivalent in strength to temperature.

The best multivariate model explaining radial growth as a function of climate ($r^2 = 0.52$, P-value for overall model and both explanatory variables < 0.01) was: standardized radial growth = 4.148 - 0.0003 (total HDD prior October to September) - 0.007 (total days with precipitation prior November to August).

The standardized residuals from this model displayed positive temporal autocorrelation (r = 0.418, P = 0.004, n = 46 between standardized residuals and year), which suggests that radial growth values predicted from the model fall short of the actual growth in the later portion of the study period. In other words, an additional driving force beyond the climate variables considered was impacting radial growth. Given the positive effects on radial growth rates of trees by CO_2 fertilization shown in other studies (e.g., Norby et al. 1999; Soulé and Knapp 2006), I added CO_2 to

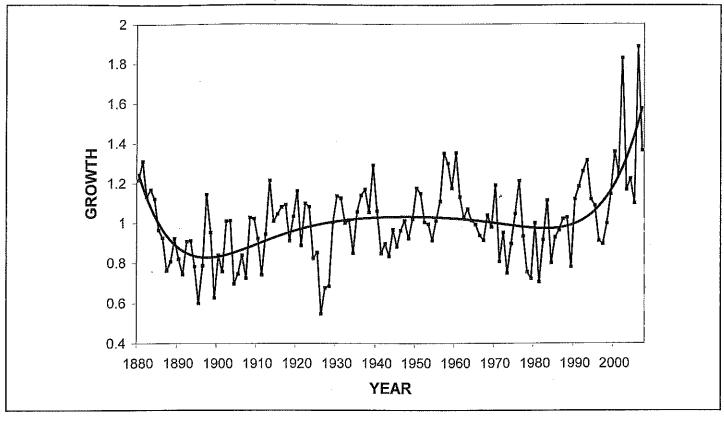


Figure 2. Standardized radial growth of red spruce (*Piçea rubens*) on GFM, 1880 to 2007. Growth is standardized to mean value of one. A 6th-order polynomial (solid black line) shows the smoothed trend.

the multivariate model and produced a second model of radial growth ($r^2 = 0.62$, P < 0.01 for the overall model and each explanatory variable):

standardized radial growth = 2.331-0.0002 (total HDD prior October to September) -0.007 (total days with precipitation prior November to August) + 0.004 (CO₂).

The residuals from this model displayed no autocorrelation.

In searching for relationships between radial growth rates of red spruce and acidic deposition, I used the TVA emissions from 1974 to 2007 as surrogate variables. Over the time period when radial growth displayed its greatest increases, SO_2 emissions dropped drastically (Figure 4), and there is a significant relationship between total emissions (base 10 log of $SO_2 + NO_X$ emissions) and radial growth for the same period (r = -0.58, P < 0.001). Incorporating the impact of total emissions and climate, the best model produced ($r^2 = 0.59$, P-value for the overall model and each explanatory

variable < 0.05) was:

Standardized radial growth = 3.978 - 0.008 (total days with precipitation prior November to August) - 0.48 (base 10 log of $SO_2 + NO_X$ emissions).

The residuals from this model displayed no autocorrelation.

Climate Change

With the exception of the variable "days with precipitation > 0.254 cm," the climate variables controlling radial growth of red spruce displayed no significant (P < 0.05) temporal trends (Table 1). However, significant temporal trends in minimum temperature, mean temperature, and HDD indicate the climate on GFM is warming, especially during the summer months (Table 2). Of these, the most dramatic trend is for warming as measured by minimum summer (June, July, August) temperature (Table 2, Figure 3). Minimum summer temperatures for the period 1998 to 2007 averaged 1.4 °C more than during the

period 1956 to 1965.

DISCUSSION

Because radial growth rates of red spruce on GFM trended positively through time (r = 0.281, P = 0.044, n = 52, Figure 2),the results of this study concur with those of Goelz et al. (1999) who also found no evidence of growth decline on nearby Mount Mitchell or Mount Rogers. The environments that support red spruce in the southern United States, including GFM, occur at high-elevation because the species requires cool and moist conditions to survive. However, within the range of temperatures experienced on GFM (mean July maximum temperature 20.6 °C; mean January minimum temperature -6.7 °C), radial growth of red spruce trees responded positively to warmer conditions, especially the cumulative effect of warmer conditions during the prior winter and current year growing season. The trees also grow faster in years where there are fewer days with precipitation. As soil moisture is unlikely

Table 1. Significant (P < 0.05) correlations between standardized radial growth and climate variables (significant correlations boldfaced). The top three relationships for each climate variable (if available) are shown. For each climate variable significantly related with radial growth, the relationship with time is shown.

Climate Variable	growth/climate			climate/time		
Mean Temperature	r-value	P-value	<u>n</u>	<u>r-value</u>	P-value	<u>n</u>
Oct. to Sept.	0.463	0.002	43	0.235	0.129	43
Prior February	0.439	0.001	50	0.150	0.300	50
Prior Oct. to Aug.	0.437	0.003	43	0.254	0.101	43
Minimum Temperature	r-value	P-value	<u>n</u>	<u>r-value</u>	P-value	<u>n</u>
Prior February	0.529	0.000	49	0.146	0.317	49
Prior Nov. to Sep.	0.507	0.001	42	0.275	0.078	42
Prior Oct. to Sep.	0.5	0.001	42	0.270	0.084	42
Maximum Temperature	r-value	P-value	<u>n</u>	r-value	P-value	<u>n</u>
Prior Oct. to Sep.	0.386	0.011	43	-0.105	0.505	43
Prior Oct. to Aug.	0.361	0.017	43	-0.061	0.697	43
June, July, Aug.	0.351	0.011	52	0.089	0.532	52
Base 65°F Heating Degree Days	r-value	P-value	<u>n</u>	r-value	P-value	<u>n</u>
Prior Oct. to Sep.	-0.517	0.000	46	-0.284	0.056	46
Prior Oct. to Aug.	-0.514	0.000	46	-0.273	0.067	46
Prior Nov. to Sep.	-0.49	0.001	46	-0.284	0.055	46
Days with Precipitation (GFM data)	r-value	P-value	<u>n</u>	<u>r-value</u>	P-value	<u>n</u>
Prior Nov. to July	-0.519	0.000	51	0.037	0.796	51
	-0.518	0.000	51	0.068	0.636	51
Prior Dec. to Aug.	-0.465	0.001	51	0.047	0.742	51
Days with ppt. > 0.254cm (NCDC)	r-value	P-value	<u>n</u>	<u>r-value</u>	P-value	<u>n</u>
Prior Nov. to Aug.	-0.524	0.000	43	-0.318	0.038	43
Prior Nov. to Jul.	-0.444	0.003	43	-0.294	0.056	43
Prior Dec. to Aug.	-0.426	0.004	44	-0.332	0.028	44
Precipitation	r-value	P-value	<u>n</u>	<u>r-value</u>	P-value	<u>n</u>
Prior July	0.414	0.003	51	0.113	0.431	51
Prior May	-0.296	0.037	50	0.007	0.962	50
Snowfall	<u>r-value</u>	P-value	<u>n</u>	<u>r-value</u>	P-value	<u>n</u>
February	-0.384	0.010	44	-0.019	0.903	44

a limiting factor for growth in as wet an environment as GFM (average annual precipitation of 132 cm), one possibility is that the days with precipitation variable is a surrogate for the cumulative effects of sunny conditions (i.e., less cloudy, rainy days), which would increase the amount of time the trees are photosynthetically active. Although both climate variables significantly impact tree growth on their own and when paired in a multivariate model, they are not significantly correlated with each

Table 2. Significant (P < 0.05) correlations between climate variables and time. The top five significant correlations (when available) for each variable are shown.

Mean Temperature	<u>r-value</u>	P-value	<u>n</u>
July	0.399	0.003	52
June, July, Aug.	0.384	0.005	52
Minimum Temperature	r-value	P-value	<u>n</u>
June, July, Aug.	0.649	0	52
July	0.592	0	52
Aug.	0.484	0	52
May, June, July	0.417	0.002	52
Sep., Oct., Nov.	0.363	0.008	52
Maximum Temperature	r-value	P-value	<u>n</u>
none			
Base 65°F Heating Degree Days	r-value	P-value	<u>n</u>
July	-0.33	0.017	52
June, July, Aug.	-0.282	0.043	52
Days with Precipitation (GFM data)	r-value	P-value	<u>n</u>
June, July, Aug.	0.348	0.012	52
June	0.346	0.012	52
Dec., Jan., Feb.	-0.298	0.034	51
February	-0.287	0.046	49
Days with ppt. > 0.254cm (NCDC)	<u>r-value</u>	P-value	<u>n</u>
Prior Dec. to April	-0.415	0.005	45
February	-0.394	0.005	49
Dec., Jan., Feb	-0.349	0.017	46
Prior Dec. to Aug.	-0.332	0.028	44
Prior Nov. to Aug.	-0.318	0.038	43
Precipitation	r-value	P-value	<u>n</u>
none ,			
<u>Snowfall</u>	<u>r-value</u>	P-value	<u>n</u>
April	-0.307	0.034	48

other (r = 0.084, P = 0.579, n = 46). The third variable included in the regression model, atmospheric CO2 concentration, was positively related to radial growth (r = 0.347, P = 0.012, n = 52) and increased the explanatory power of the model by

10%. The effects of CO₂ fertilization on the growth rates of trees are usually best developed in semiarid environments (e.g., Soulé and Knapp 2006) where changing stomatal conductance caused by increasing CO₂ in turn increases water-use efficiency.

Although GFM is not a moisture-limited environment, increasing CO2 has been shown to enhance photosynthesis and the subsequent growth rates of trees in a variety of ecosystems and climatic regimes (e.g., Norby et al. 1999; Ainsworth and Long 2005).

Many of the spruce-fir ecosystems on high elevation peaks in the southern Appalachian Mountains were reported to be in a state of decline in the late 20th century, including peaks in the Great Smoky Mountains (McLaughlin et al. 1987) and nearby Mt. Mitchell (Bruck 1989; Silver 2003). Multiple, synergistic causes for the decline were likely and included negative impacts from the spread of the balsam wooly adelgid [Adelges picae (Ratzeburg)] (Cook and Zedaker 1992), climatic stressors such as drought and ice storms (Cook and Zedaker 1992; Busing 2004), and the negative effects of acidic deposition (McLaughlin et al. 1987). Although limited evidence of a late 20th century forest decline exists for GFM (e.g., Bruck 1989), the late Hugh Morton, former President of GFM, was concerned about possible relationships between acidic deposition and visible decline of the ecosystem in the late 1980s. An exhibit containing repeat photographs Morton took showing ecosystem decline from 1964 to 1990 is still a part of the nature museum on GFM, and he recruited Walter Cronkite to narrate a PBS documentary titled "The Search for Clean Air" in 1995 that dealt with the issue of acid rain damage to high elevation forests in the eastern United States (see http://www.grandfather.com/press_room/ HMM/HMM_bio.php>).

Although the proxy data I used to identify potential impacts of acidic deposition on the high elevation spruce-fir ecosystem on GFM are limited both temporally and spatially, the significant relationship suggests that upwind emissions of high quantities of SO2 and NOx may have been detrimental to radial growth rates of red spruce. In response to the establishment of National Ambient Air Quality Standards as part of the Clean Air Act of 1970 (and subsequent amendments to the act), TVA and other sources have significantly reduced emissions of SO₂ and NO_X (Figure 4). Post-

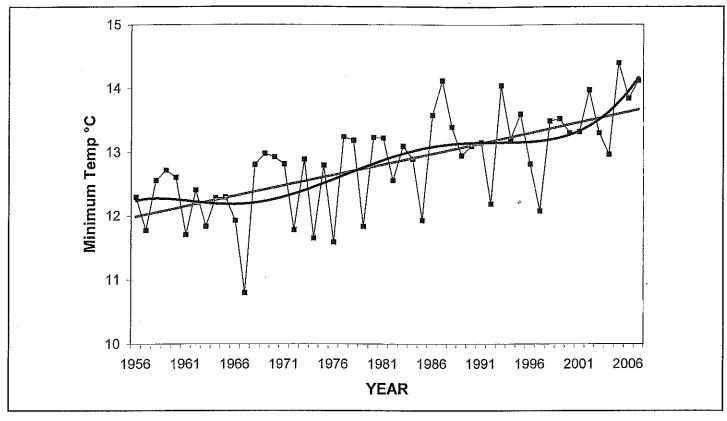


Figure 3. Minimum summer (June, July, August) temperatures on GFM, 1956 to 2007 (squares). A 6th-order polynomial (black line) shows the smoothed trend and the linear trend is shown by the hatched line.

1950s radial growth rates of red spruce reached their minimum values in the late 1970s to early 1980s, but have generally increased since that time, concurrent with the steady decline of emissions: an intriguing finding given the body of research linking acidic deposition to spruce-fir forest decline in the late 20th century.

While many of the significant temporal trends in climatic conditions over the last 52 years are weak (i.e., r-values < 0.4, Table 2), the summertime trends in minimum temperatures are dramatic. The large increases in minimum temperature relative to maximum temperature mirror global trends (Easterling et al. 1997; Vose et al. 2005), but because GFM is a protected area, the cause of the warming cannot be simply attributed to land use/land cover changes. While increasing cloud cover is mentioned as a possible cause of minimum temperature increases (Easterling et al. 1997), the trend data from GFM on days with precipitation (a surrogate variable for cloud cover) are mixed (Table 2). In

addition to stimulating radial growth of trees, increasing temperatures may alter the spruce-fir ecosystem in unpredictable ways on GFM. Globally, the most notable ecosystem change attributed to warming temperature is a poleward advance of the boreal tree line (Grace et al. 2002), but other changes involving species richness and diversity (e.g., Thuiller et al. 2006) and elevational changes in ecosystem composition (e.g., Kullman 2001) have been explored. For coniferous trees, results from predictive modeling studies suggest that habitats may shrink with continued warming (e.g., Hamann and Wang 2006). For GFM, one of the primary concerns is that sustained warming may ultimately cause a vertical advance of the mixed deciduous forest that is the late-successional vegetation on GFM's lower slopes. In turn, this would lead to a reduction in size of the spruce-fir ecosystem and a subsequent loss of species and ecosystem diversity.

CONCLUSIONS

Growth rates of high elevation red spruce trees growing on GFM have changed in recent decades, with a trend toward above-average radial growth in the past two decades. Using regression modeling, I linked the pattern of radial growth change since the mid-1950s to both climatic and atmospheric drivers. Two intriguing findings are that the trees responded positively to warmer temperatures within the range of temperatures found on the higher elevations of GFM and that temperatures on the mountain were trending significantly upward. The observed warming on GFM appears to be positively impacting red spruce, and other driving forces, including increasing CO2 and decreasing rates of emissions contributing to acidic deposition, also are linked to increasing radial growth rates. While all of the driving forces for radial growth of red spruce on GFM appear to be vectoring in a positive fashion, radial growth is only one of a large suite of measures of potential ecosystem response

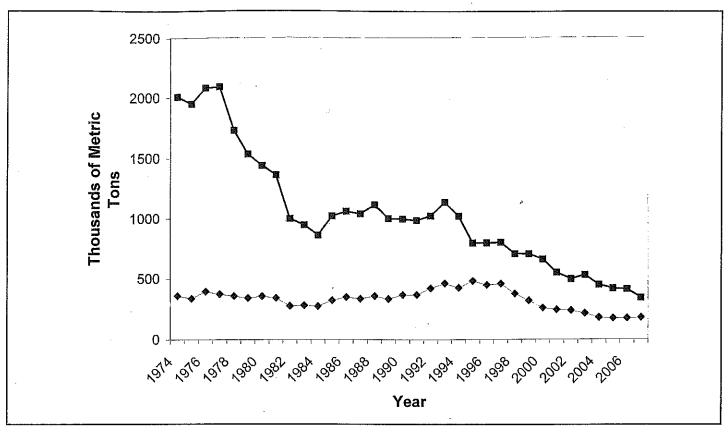


Figure 4. Emissions of SO₂ (squares) and NO_X (diamonds) from the Tennessee Valley Authority, 1974 to 2007 (Available online at www.tva.com/environment/air/totaldata.htm).

to changes in climate and atmospheric composition. The spruce-fir forest on GFM is one of a handful of rare and disjunct ecosystems found only in the highest elevations of the southern Appalachian Mountains because of the cool and moist conditions these conifers need to survive. If the dramatic warming being experienced on GFM continues, it could potentially lead to local extirpations of both plant and animal species and a contraction of the spatial extent of this ecosystem in the southern Appalachians.

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LITERATURE CITED

Adams, H.S., S.L. Stephenson, T.J. Blasing, and D.N. Duvick. 1985. Growth-trend declines of spruce and fir in mid-Appalachian subalpine forests. Environmental and Experimental Botany 25:315-325.

Ainsworth, E.A., and S.P. Long. 2005. What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. New Phytologist 165:351-372.

Anderson, J.B., R.E. Baumgardner, V.A. Mohnen, and J.J. Bowser. 1999. Cloud chemistry in the eastern United States, as sampled from three high-elevation sites along the Appalachian Mountains. Atmospheric Environment 30:5105-5114.

Arp, P.A., and J. Manasc. 1988. Red spruce stands downwind from a coal-burning power generator: tree ring analysis. Canadian Journal of Forest Research 18:251-264.

Bruck, R.I. 1989. Forest decline syndromes in the southeastern United States. Pp. 113-190 in J.J. MacKenzie and M.T. El-Ashry, eds., Air Pollution's Toll on Forests and Crops. Yale University Press, New Haven, Conn.

Bruck, R.I., and W.P. Robarge. 1988. Change in forest structure in the boreal montane ecosystem of Mount Mitchell, North Caro-

- lina. European Journal of Forest Pathology 18: 357-366.
- Burns, R.M., and B.H. Honkala (tech. coords.).
 1990. Silvics of North America: 1. Conifers;
 2. Hardwoods. Agriculture Handbook 654,
 U.S. Department of Agriculture, Forest
 Service, Washington, DC. Available online
 <www.na.fs.fed.us/pubs/silvics_manual/
 volume_1/picea/rubens.htm>. Accessed 10
 February 2010.
- Busing, R.T. 2004. Red spruce dynamics in an old southern Appalachian forest. Journal of the Torrey Botanical Society 131:337-342.
- Cook, E.R., and R.L. Holmes. 1997. ARSTAN: Chronology development. Pp. 75-92 in H.D. Grissino-Mayer, R.L. Holmes, and R.L. Fritts, eds., The International Tree-Ring Data Bank Program Library, Version 21 User's Manual. University of Arizona Laboratory of Tree-Ring Research, Tucson.
- Cook, E.R., and S.M. Zedaker. 1992 The dendroecology of red spruce decline. Pp. 192-231 in C. Eagar and M.B. Adams, eds., Ecology and Decline of Red Spruce in the Eastern United States. Springer-Verlag, New York.
- DeLucia, E.H., J.G. Hamilton, S.L. Naidu, R.B. Thomas, J.A. Andrews, A. Finzi, M. Lavine, R. Matamala, J.E. Mohan, G.R., Hendrey, and W.H. Schlesinger. 1999. Net primary production of a forest ecosystem with experimental CO2 enrichment. Science 284:1177-1179.
- Drake, B.G., and M.A. Gonzalez-Meler. 1997. More efficient plants: a consequence of rising atmospheric CO2? Annual Review of Plant Physiology and Plant Molecular Biology 48:609-639.
- Driscoll, C.T., G.B. Lawrence, A.J. Bulger, T.J. Butler, C.S. Cronan, C. Eagar, K.F. Lambert, G.E. Likens, J.L. Stoddard, and K.C.Weathers. 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. BioScience 51:180-198.
- Easterling, D.R., B. Horton, P.D. Jones, T.C. Peterson, T.R. Karl, D.E., Parker, M.J. Salinger, V. Razuvayev, N. Plummer, P. Jamason, and C.K. Folland. 1997. Maximum and minimum temperature trends for the globe. Science 277:364-367.
- [EC] Environment Canada. 2010. Acid Rain and the Facts. Available online <www.ec.gc.ca/acidrain/acidfact.html> Accessed 10 February 2010.
- Etheridge, D.M., L.P. Steele, R.L. Langenfelds, R.J. Francey, J.-M. Barnola, and V.I. Morgan. Historical CO2 records from the Law Dome DE08, DE08-2, and DSS ice cores. In Trends: a compendium of data on

- global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn.
- Goelz, J.C.G., T.E. Burk, and S.M. Zedaker. 1999. Long-term growth trends of red spruce and fraser fir at Mt. Rogers, Virginia and Mt Mitchell, North Carolina. Forest Ecology and Management 115:49-59.
- Grace, J., F. Berninger, and L. Nagy. 2002. Impacts of climate change on the tree line. Annals of Botany 90:537-544.
- Hamann, A., and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2773-2786.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43:69-78.
- Kullman, L. 2001. 20th century climate warming and tree-limit rise in the southern Scandes of Sweden. Ambio 30:72-80.
- Laurence, J.A., R.G. Amundson, R.J. Kohut, and D.A. Weinstein. 1997. Growth and water use of red spruce (Picea rubens Sarg.) exposed to ozone and simulated acidic precipitation for four growing seasons. Forest Science 43:355-361.
- LeBlanc, D.C., N.S. Nicholas, and S.M. Ze-daker. 1992. Prevalence of individual-tree growth decline in red spruce populations of the southern Appalachian Mountains. Canadian Journal of Forest Research 22:905-914.
- Little, C.E. 1997. The Dying of the Trees. Penguin Books, New York.
- Mooney, H.A., B.G. Drake, R.J. Luxmoore, W.C. Oechel, and L.F. Pitelka. 1991. Predicting ecosystem responses to elevated CO2 concentrations. BioScience 41:96-104.
- McLaughlin, S.B., D.J. Downing, T.J. Blasing, E.R. Cook, and H.S. Adams. 1987. An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the Eastern United States. Oecologia 72:487-501.
- [NCDC] National Climatic Data Center. 2008a. Available online http://wwwJ-StnSrch~StnID~20013974 Accessed 30 July 2008.
- [NCDC] National Climatic Data Center. 2008b. Available online http://wwwDI~DatasetSearch~3200~313565~20013974 Accessed 30 July 2008.
- Norby R.J., S.D. Wullschleger, C.A.Gunderson, D.W. Johnson, and R. Ceulemans. 1999. Tree responses to rising CO2 in field experiments: implications for the future forest.

- Plant, Cell and Environment 22:683-714.
- Phipps, R.L. 1985. Collecting, preparing, crossdating, and measuring tree increment cores. Water Resources Investigations Report 85-4148, United States Geologic Survey, Reston, Va.
- Pitelka, L.F., and D.J. Raynall. 1989. Forest decline and acidic deposition. Ecology 70:2-10.
- Rebbeck, J., K.F. Jensen, and M.S. Greenwood. 1993. Ozone effects on grafted mature and juvenile red spruce: photosynthesis, stomatal conductance, and chlorophyll concentration. Canadian Journal of Forest Research 23:450-456.
- Silver, T. 2003. Mount Mitchell and the Black Mountains: an Environmental History of the Highest Peaks in Eastern America. University of North Carolina Press, Chapel Hill.
- Soulé, P.T., and P.A. Knapp. 2006. Radial growth rate increases in naturally-occurring ponderosa pine trees: a late 20th century CO2 fertilization effect? New Phytologist 171:379-390.
- Stephenson, S.L., and H.S. Adams. 1995. A comparative study of spruce growth rates in four different regions of the world. Virginia Journal of Science 46:25-34.
- Stokes, M.A., and T.L. Smiley. 1996. An Introduction to Tree-ring Dating. University of Arizona Press, Tucson.
- Tager, M. 1999. Grandfather Mountain: a Profile. Parkway Publishers, Boone, N.C.
- Thornton, F.C., J.D. Joslin, P.A. Pier, H. Neufeld, J.R. Seiler, and J.D. Hutcherson.1994. Cloudwater and ozone effects upon high elevation red spruce: a summary of study results from Whitetop Mountain, Virginia. Journal of Environmental Quality 23:1158-1167.
- Thuiller, W., S. Lavorel, M.T. Sykes, and M.B. Araujo. 2006. Using niche-based modeling to assess the impact of climate change on tree functional diversity in Europe. Diversity and Distributions 12:49-60.
- Volin, J.C., P.B. Reich, and T.J. Givnish. 1998. Elevated carbon dioxide ameliorates the effects of ozone on photosynthesis and growth: species respond similarly regardless of photosynthetic pathway or plant functional group. New Phytologist 138:315-325.
- Vose, R.S., D.R. Easterling, and B. Gleason. 2005. Maximum and minimum temperature trends for the globe: an update through 2004. Geophysical Research Letters 32, doi: 10.1029/2005GL024379, 2005.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research 21:414-416.