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ORIGINAL ARTICLE

Impacts of human disturbance on the temporal stability of climate–growth relationships in a red spruce forest, southern Appalachian Mountains, USA

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ABSTRACT

We used dendrochronological techniques to develop a tree-ring chronology (AD 1874–2009) from live trees and investigated the temporal stability of regional climate signals in the heavily disturbed red spruce (*Picea rubens* Sarg.) and Fraser fir [*Abies fraseri* (Pursh) Poir.] forest of Roan Mountain, Tennessee and North Carolina, USA. We performed bootstrapped correlation analyses in split data sets and moving intervals analyses to detect shifts in climatic sensitivity during periods of changing forest structure following disturbances. Most notably, a significant shift in red spruce temperature sensitivity occurred post-1930s, where positive growth responses to warm temperatures shifted to negative responses, and this shift coincided with a period of clearcut harvesting. As exogenous disturbances (i.e. ice storms, wind throw, and acidic deposition) are expected to continue altering the structure of this forest throughout the region, the climatic sensitivity of these species may become increasingly unstable.

Introduction

The red spruce (*Picea rubens* Sarg.)-Fraser fir [*Abies fraseri* (Pursh) Poir.] (RSFF) forest community exists in only a few disjunct, high-elevation island populations of the southern Appalachian Mountains. Human-induced climate change has influenced these forests (Cook and Johnson, 1989; Webster et al., 2004). During the mid-20th century, RSFF forests in the southern Appalachian Mountains experienced widespread growth decline and tree mortality (Hornbeck and Smith, 1985; Adams and Eagar, 1992). Determining a single cause for 20th century red spruce decline is difficult because forests are complex systems that are subjected to multiple stresses (Cook and Johnson, 1989; Pitelka and Raynal, 1989), and the red spruce decline is likely related to a combination of pollution, acidic deposition, insect outbreaks, and human alterations to the environment (Cook and Johnson, 1989; Mohnen, 1990; Adams and Eagar, 1992; Webster et al., 2004; Nowacki et al., 2010; Koo et al., 2011). Climate change also could detrimentally affect red spruce populations through temperature stress (McLaughlin et al., 1987; Cook and Johnson, 1989). The health and vigor of the disjunct RSFF forests in the southern Appalachian Mountains is causing concern among ecologists, land managers, and the public (Rentch et al., 2010; White et al., 2012) as these forests are valued for both economic and ecological reasons. The Great Smoky Mountains National Park is the most visited National Park in the United States, and the park and surrounding National Forests are a popular recreational destination for millions of tourists, travelers, and hikers each year (NPS, 2008; USDA, 2008b). Researchers value the forest because of its renowned biodiversity and rare plant populations.

Growth of red spruce and other tree species that exist at high elevations and latitudes are thought to be primarily limited by temperature (Fritts, 1976). Trees existing nearest the limit of their range are believed to be more climatically sensitive because their habitat is more limiting (Fritts et al., 1965). Prevailing dendroclimatic thought would assume that disjunct populations of red spruce along the peaks of the southern Appalachian Mountains would be among the most temperature sensitive of the species. Though dendroclimatologists have found red spruce to be a useful indicator of climate change, little research with the species has taken place in the southern Appalachian Mountains since the 1980s (Cook, 1988; Webster et al., 2004; Koo et al. 2011).

The highest elevations of the southern Appalachians receive significant amounts of moisture from cloud and fog cover in addition to precipitation (Mohnen, 1990, 1992). Therefore, moisture does not typically limit tree growth at high elevations (Webster et al., 2004). Temperature is unstable compared to precipitation in high-elevation forests (Fritts, 1976). Red spruce in the southern Appalachians exists very near its temperature threshold,

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as evidenced by the conflicting or diminishing temperature signals observed between high and low elevation red spruce populations (Cook et al., 1987; Johnson et al., 1988; Webster et al., 2004; Koo et al., 2011).

The relationship between high-elevation tree species and climate may be unstable through time (Jacoby and D'Arrigo, 1995; Briffa, 2000; D'Arrigo et al., 2004, 2008). Divergence can exist between instrumentally recorded climate data and tree-ring derived climate inferences (D'Arrigo et al., 2008; Esper and Frank, 2009). The divergence problem has developed into a major concern in dendroclimatology, as it calls into question the validity of dendroclimatological principles and data analyses for climate reconstructions (D'Arrigo et al., 2008). Time series analysis is a necessary component of climate–radial growth relationship studies to avoid erroneous predictions of past climate. The presence of a divergence between climate and tree growth may be specific to characteristics of a particular site or species (D'Arrigo et al., 2008), accentuating the importance of understanding disturbance regimes when studying climate–growth relationships. Red spruce dendroclimatology studies in its northern range have confirmed that the species is temperature sensitive (Cook et al., 1987). However, the long-term temperature–radial growth relationships in red spruce are not temporally stable in the northeastern United States (Cook et al., 1987; Johnson et al., 1988; Smith and Nicholas, 1999), and in low-elevations of the Great Smoky Mountains National Park in the southern Appalachian Mountains (Webster et al., 2004; Koo et al., 2011).

Among the highest peaks of the southern Appalachian Mountains, Roan Mountain hosts one of the RSFF forest communities found within the region. Roan Mountain has experienced land-use changes and disturbances that have greatly affected the ecology the RSFF forest (Laughlin, 1991; Wilson, 1991; White et al., 2012). The Roan Mountain RSFF forest has been heavily disturbed during the past century (Laughlin, 1991; Wilson, 1991; White et al., 2012). Intensive logging operations on the mountain during the 1930s (Wilson, 1991) and repeated balsam wooly adelgid (*Adelges piceae*) infestations have affected forest community structure (Dull et al., 1988; Potter et al., 2005; Koo et al., 2011). Because land-use history can affect the stability of the climate signal in high-elevation red spruce trees (Webster et al., 2004), we explored how the relationship between climate and disturbance influenced red spruce radial growth over time. Thus, this investigation fills a gap in our understanding of climate–disturbance interactions in high-elevation, red spruce trees in the southern Appalachian Mountains. Specifically, our research questions address:

(1) Are climatic factors the primary regulators of red spruce radial growth at Roan Mountain, or has excessive disturbance overridden the influence of climate over radial growth?
(2) Is a red spruce climate signal strong and temporally stable, or does the climate response change over time?

Study area

Roan Mountain is a part of the Unaka Mountains, a subset of the southern Appalachian Mountains and part of the Blue Ridge physiographic province (Clark, 2008). The mountain is located at approximately 36°6′16.42″ N, 82°7′47.39″ W (Fig. 1). Roan Mountain (including Roan High Bluff and Roan High Knob) encompasses approximately 19 km^2. Roan Mountain is jointly managed by the Pisgah National Forest in North Carolina and the Cherokee National Forest in Tennessee. The high elevation of Roan Mountain (1919 m) results in cooler temperatures, increased precipitation, and higher wind speed than the surrounding lower elevations (Brown, 1941). Climatic normals for the 1981–2010 period show a mean annual temperature of 8.7 °C and total precipitation of 141 cm (PRISM, 2010). Soils are primarily well-drained inceptisol loams that form on steep, rocky slopes and ridge tops (NRCS, 2010).

The Roan Mountain RSFF was surveyed prior to 1930s logging (Brown, 1941) and red spruce and Fraser fir were found to represent 89.2% of all trees (62.3% Fraser fir and 26.9% red spruce). Yellow birch (*Betula alleghaniensis)* Britt., mountain maple (*Acer spicatum)* Lam., mountain ash (*Sorbus americana)* Marsh., American beech (*Fagus grandifolia)* Ehrh., yellow buck eye (*Aesculus octandra)* Aiton, and pin cherry (*Prunus pensylvanica)* L. were also present and now make up <1% of the forest. The current forest community is in an early- to mid-successional stage dominated by dense Fraser fir regeneration in the undergrowth layer. The upper canopy is composed of specimens that were likely undesirable to loggers and that subsequently thrived in the post-logging environment. Other species present during the pre-logging period are virtually nonexistent today. Outbreaks in balsam wooly adelgid infestation have occurred periodically, but are thought to be of low severity because of the juvenile nature of Fraser fir during post-logging regeneration (White et al., 2012).

Methods

Red spruce chronology development

We collected increment cores for dendrochronological analysis from red spruce trees in the Roan Mountain study area. We collected, mounted, and sanded all red spruce cores following standard dendroecological techniques (Stokes and Smiley, 1996). We dated and visually crossdated all red spruce cores. We measured annual growth rings from red spruce trees (series) to the nearest 0.001 mm with a Velmex measuring system coupled with Measure J2X software. We used 30-year segments lagged successively by 15 years using the computer program COFECHA to verify crossdating accuracy of each red spruce series (Holmes, 1983; Grissino-Mayer, 2001). The chronology incorporated red spruce increment cores from a previous forest succession study at Roan Mountain (White et al., 2012) as well as supplemental red spruce cores collected for the purpose of this study. 15 cores from 14 red spruce specimens were included from the previous study plots, and the remaining supplementary 13 cores from 8 trees were collected from the broader study area surrounding the plots for red spruce chronology development. Due to the difficult nature of crossdating southern red spruce, we elected to use the highest correlated individual cores for the chronology. The final Roan Mountain red spruce chronology (RMS) chronology included 28 core samples from 22 trees.

We standardized red spruce series to remove effects from age-related growth trends that could add noise to the series unrelated to the climate signal desired in chronology development (Fritts, 1976). We removed the age-related growth trend of each sample using the program ARSTAN (Cook, 1985), which fits a negative exponential trend line to the growth of the sample using the least squares technique (Fritts, 1976; Cook, 1985). A negative exponential trend line was suitable because the oldest samples grew primarily during the open, early-successional era following the intense logging period. The indices were then averaged for each year across all series to create a single red spruce chronology (Fritts, 1976).

Instrumental climate data

We analyzed the red spruce growth–climate relationship using National Climatic Data Center (NCDC) divisional data for the North

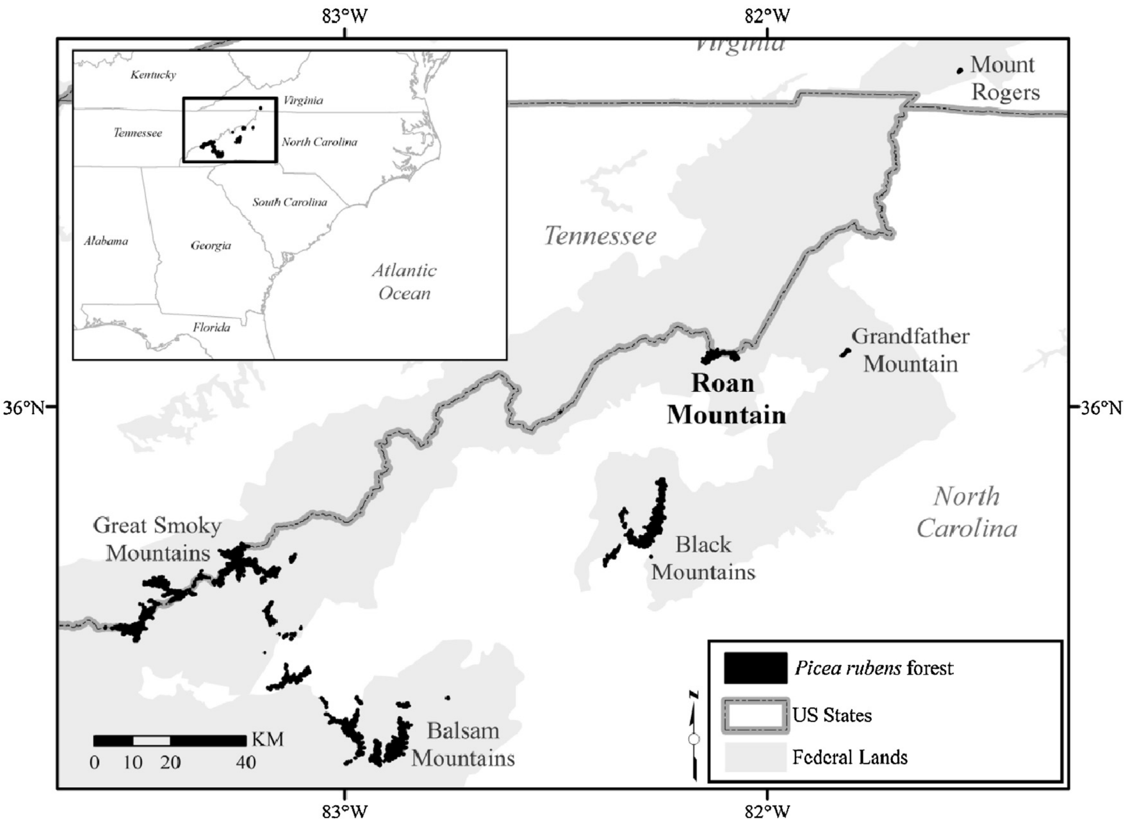

Fig. 1. Red spruce (*Picea rubens* Sarg.) high-elevation disjunct forests in the southern Appalachian Mountains, USA. This study was conducted on Roan Mountain in North Carolina.

Carolina Northern Mountains climate division (NCDC, 2010). We obtained monthly average temperatures, monthly precipitation totals, and monthly Palmer Drought Severity Index (PDSI) values for the period 1896–2008. PDSI is a water balance-based index that quantifies the intensities of dry and wet periods (Palmer, 1965). As temperature and water availability often form the primary link between climate and tree physiological processes, dendrochronologists often use these variables when assessing the growth–climate relationship (Fritts, 1976).

Correlation analysis

We used DENDROCLIM2002 (Biondi and Waikul, 2004) to perform a split data correlation analysis and a moving interval analysis. This allowed us to detect both shifts in climatic sensitivity (i.e. gradual or abrupt changes) and fluctuations in the strength of a climate signal (i.e. a weakening and strengthening of the climate–growth relationship). We tested monthly climate variables for a span of months beginning with April of the previous year and ending with October of the current year (19-month period – previous April to current October). Previous months were included to compare the lagged responses of the previous and current year growing seasons. We omitted the earliest year (1895) of the instrumental climate datasets from this analysis because no data exists of the previous seasonal climatic variables for this initial year. In the moving interval analysis, we tested the entire climate period (1896–2008) to determine when radial growth–climatic relationships were strongest during the instrumental climate record. Our moving interval period was double the number of monthly climate variables (38 years), thus the period of results from the correlation analysis was 1933–2008.

To help determine if the extensive logging of the 1930s had any impacts on the response of radial tree growth to climate, we split the data set into pre- (1896–1930) and post-logging (1940–2008) era subsets and examined relationships between the same suite of monthly climatic variables using bootstrapped correlation. We then compared the climate responses pre- and post-logging era.

Results

Roan mountain red spruce chronology

The RMS chronology was 136 years in length, spanning from 1874 to 2009 (Fig. 2). The Standard chronology consisted of 28

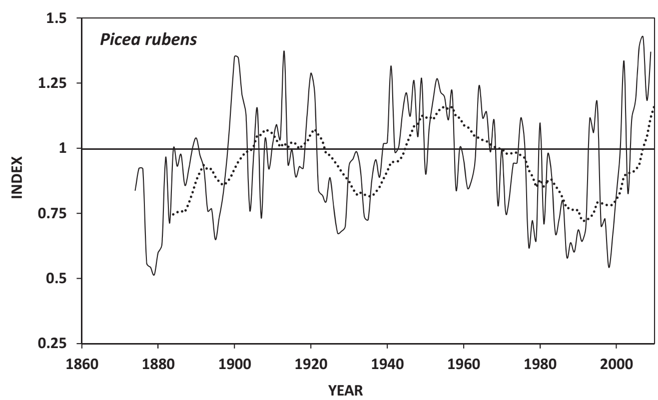

Fig. 2. Radial growth chronology (index) from red spruce (*Picea rubens* Sarg.) trees at Roan Mountain, North Carolina (AD 1874–2009). The mean radial growth is standardized to 1.0 and the dashed line is the 10-year moving average.

dated tree-ring series with 2762 rings in total. The mean length of all series in the chronology was 98.6 years, and the oldest dated sample was 135 years old. The interseries correlation of the RMS chronology was 0.551 ($p \leq 0.01$), while the mean sensitivity was 0.252. These measures compared favorably to other red spruce chronologies developed from the southern Appalachian Mountains (ITRDB, 2010) and are considered reasonably strong for tree-ring chronologies from the eastern United States (Grissino-Mayer, 2001). High interseries correlation and mean sensitivity coupled with the low autocorrelation (−0.046) of the chronology were indicative of a climatically-sensitive data set.

Climate response

The pre- and post-logging era correlation analysis revealed some dramatic shifts in climate response (Fig. 3). Overall, temperature had the greatest control on radial growth, with several months displaying significant ($p < 0.05$) relationships (Figs. 3 and 4). The strongest relationship was positive and occurred in the current year July during the pre-logging era, and the climatic response in July switched to a weaker but significantly negative response in the post-logging era (Fig. 5). Further, significant relationships that existed prior to 1930 disappeared post-logging (e.g., prior October), and new relationships emerged (e.g., prior July). Radial growth responses to precipitation and moisture availability (i.e., PDSI) also produced some shifts from positive to negative between eras, although only one relationship was statistically significant (current year May precipitation and May PDSI).

Moving correlation analysis revealed unstable relationships between red spruce growth and both precipitation and PDSI variables. We found a negative May precipitation relationship during 17 of the 112 years tested (Fig. 5), and a relatively strong negative relationship between growth and previous October precipitation from 1964 to 1987, and with April precipitation from 1959 to 1971. There were significant negative PDSI–growth relationships during the current May (primarily from 1959 to 1976) and prior October (1965–1979) (Fig. 5). We also detected an emerging trend of significant positive relationships between growth and PDSI during late-summer months. Beginning in 1993 and lasting through 2007, we found relationships between PDSI and radial growth during the previous August, September, and, to a lesser extent, July.

Discussion

In the high elevations of the Roan Mountain RSFF forests, ample orographic fog and precipitation during summer months ensure that sufficient amounts of moisture are readily available, thus the radial growth response to temperature is logical. The most apparent climate signal we found was the negative relationship between red spruce radial growth and temperature during the previous summer, with warmer summer temperatures resulting in reduced growth during the following growing season (Figs. 3 and 4). The presence of a previous-summer negative temperature signal supports previous findings of red spruce dendroclimatology research (Cook et al., 1987; Johnson et al., 1988). Warmer than average previous-late summer temperatures prolongs the growing season, which can affect the following growing season. Trees may have consumed nutrient reserves that are usually stored for the following season late in the prolonged growing season. Such an occurrence leaves little stored growth-inducing carbohydrates for early portions of the next growing season (Fritts, 1976). Alternatively, a prolonged growing season also may cause a delay of frost hardening, resulting in a greater susceptibility to tissue damage during early winter storms (Fritts, 1976; Eagar and Adams, 1992; Schaberg,

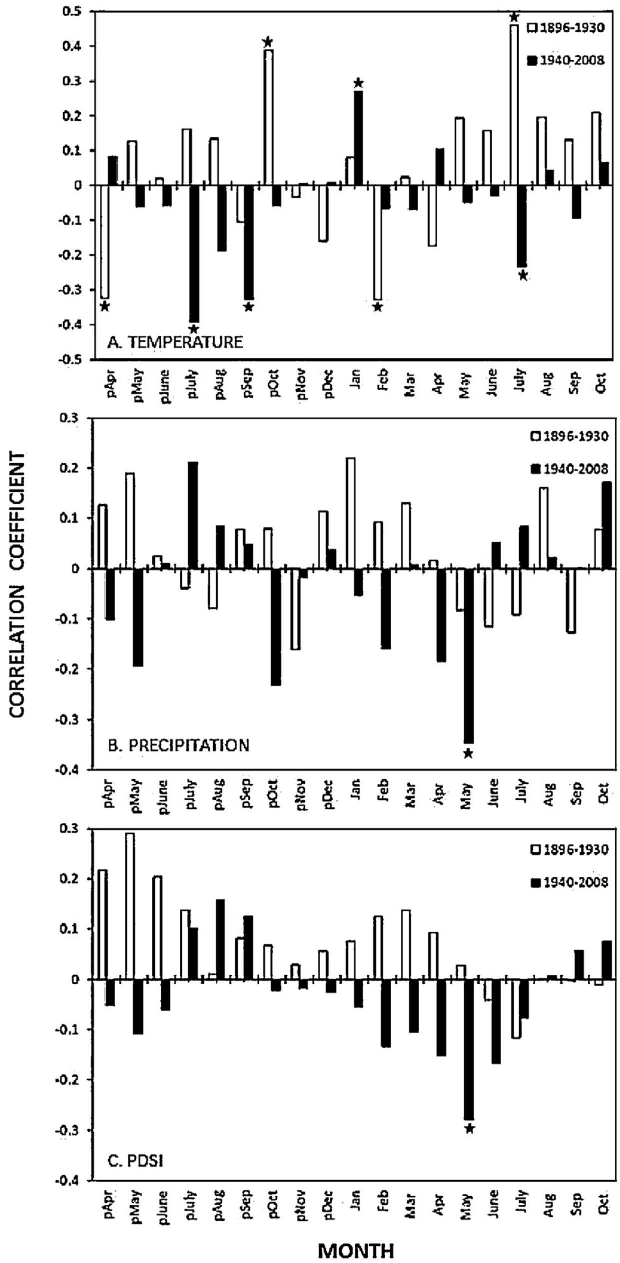

Fig. 3. Bootstrapped correlation analysis between temperature (A), precipitation (B), the Palmer Drought Severity Index (C), and red spruce radial growth. We split the data set into pre- (1896–1930) and post-logging (1940–2008) eras. The monthly variables are listed on the *x*-axis, with variables preceded by "*p*" representing months from the previous growing season.

2000). The relationship between prior summer temperature and radial growth was weakly positive and non-significant prior to the 1940s, as the forest canopy was denser, thus allowing less radiational energy to reach the forest floor.

The temperature/growth relationship evolved and progressively strengthened during the early portion of the post-logging era and is likely associated with increasing receipt of insolation. The previous summer temperature growth relationship begins to weaken (Fig. 4) with red spruce regeneration and recruitment during the late 20th and early 21st century (White et al., 2012). Thus, canopy removal associated with logging likely accentuated the growth effects linked to temperature. Another shift in climate response pre- and post-logging is evident in July (Fig. 5). During

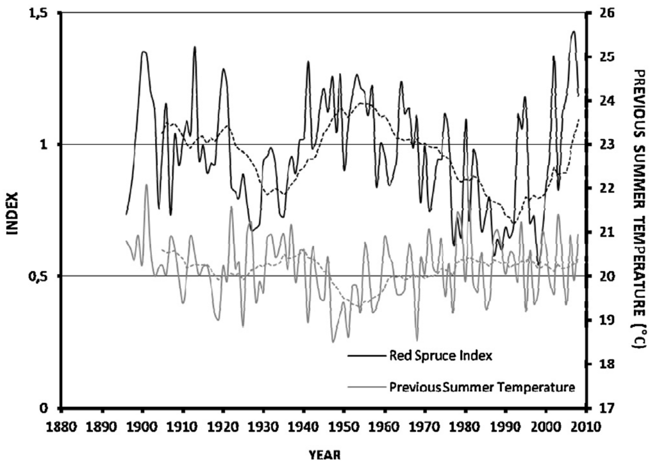

Fig. 4. Red spruce (*Picea rubens* Sarg.) chronology (index) compared to the prior year's mean summer (July–September) temperature (°C) from 1896 to 2008. The mean radial growth is standardized to 1.0 and the dashed lines are the 10-year moving averages.

July, excessively high temperatures speed plant respiration, which may cause consumption of available food at a rate that exceeds replenishment of food stores (Fritts, 1976; Schaberg et al., 2000), resulting in reduced radial growth.

In the pre-logging era winter (February) temperatures were negatively correlated with temperature, and this switched to a positive relationship (January) in the post-logging era (Fig. 5). Warm February temperatures can create a false start for the Spring months via cambial reactivation and later bud damage (Mäkinen et al., 2000; Wilmking and Myers-Smith, 2008), resulting in reduced radial growth for the year. Alternatively, warmer winter temperatures increase soil temperatures and allow moisture to infiltrate the soil (Fritts, 1976; Schwarz et al., 1997), resulting in a net increase in photosynthesis during the early growing season and a positive response with radial growth. We speculate that the later process became important within the ecosystem for a period of years post-logging related to a substantial increase in ground-level receipt of radiational energy, but would eventually weaken with maturation of the second growth forest. The positive relationship with radial growth is first identified by the moving correlation analysis in the late 1970s, which matches with the 38-year rolling window used by DENDROCLIM2002 (Fig. 5), and then weakens circa 1990.

The broad disturbance history on Roan Mountain likely influenced the unstable climatic sensitivity of the RMS chronology. The observed shift in temperature sensitivity that occurred during the 1940s coincided with a period of dramatically altered stand dynamics resulting from logging. Disturbance is known to affect climatic response of trees (Fritts, 1976), and these events were likely related. In the aftermath of the clearcut logging of the 1930s, we found a distinct period of insensitivity to climate during the 1940s, followed by the onset of the previous-summer negative temperature-growth relationship circa 1950. During the late 1930s and 1940s, the unlogged red spruce trees experienced stand-wide release events that seemingly mitigated the influence of climate (White et al., 2012). As post-logging release events tapered off and the forest canopy began to recover in the 1950s, the influence of climate on radial growth increased. One possible explanation for the mid-20th century shift in climate–growth sensitivity is the dramatic influx of solar radiation following clear-cutting. Post clearcutting, the sparse canopy conditions likely resulted in significantly warmer surface air temperatures, creating the negative previous-summer temperature signal. Alternatively, the dense regeneration and rapid influx

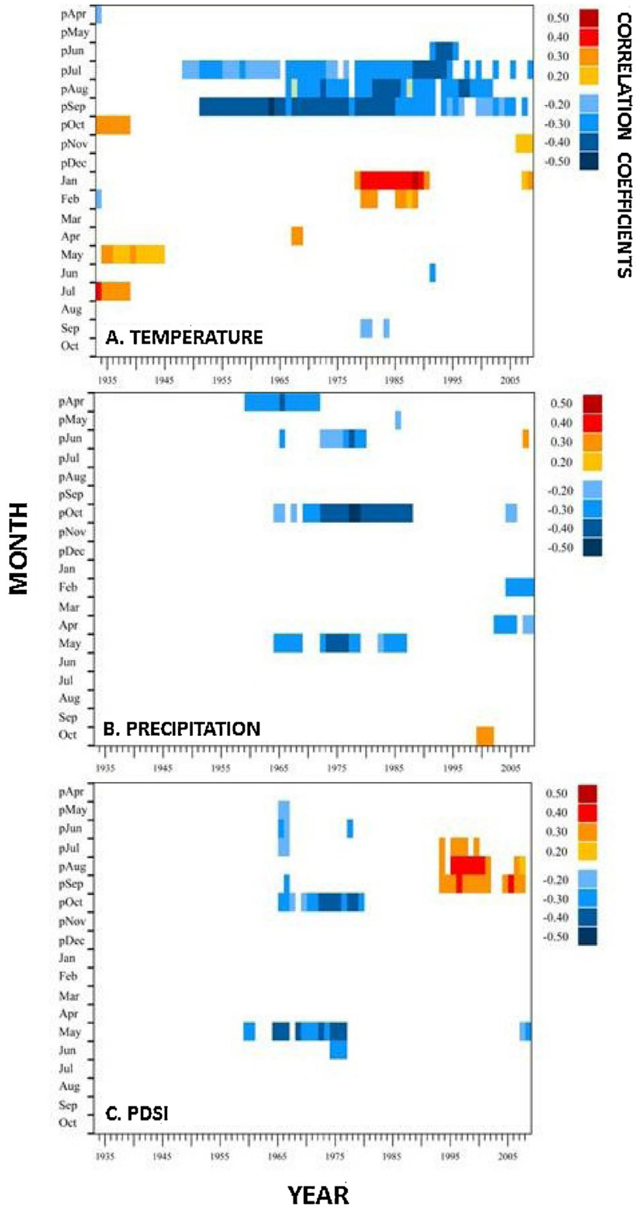

Fig. 5. Moving interval correlation analysis between temperature, precipitation, the Palmer Drought Severity Index (PDSI), and red spruce radial growth. Monthly variables are listed on the *y*-axis, with variables preceded by "*p*" representing months from the previous growing season. The final years of each progressing 38-year interval are represented on the *x*-axis. Red shades indicate direct significant relationships while blue shades represent inverse significant relationships. Strengths of correlations increase with darker hues. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of Fraser fir into the canopy may have also caused a shift in red spruce sensitivity. By the 1950s, the red spruce trees remaining in the ecosystem post-logging would have been less competitive for sunlight within a heavily shaded understory created by increased density of Fraser firs.

Aside from the 1940s and 50s sensitivity shift, the only other period when disturbance and changes in climate response co-occurred was around the year 2000. We observed a weakening of the negative previous-summer temperature relationship, an emergence of a positive previous summer drought relationship, and an increase in localized disturbance in the 1990s culminating with a stand-wide event in the year 2000. The root cause of this disturbance is unclear, but the balsam wooly adelgid may be a factor (Koo et al., 2011). A severe adelgid infestation during the 1990s would have caused many tree deaths over a period of a decade, resulting in stand-wide openings in the canopy. The resulting influx of solar radiation to the understory could have resulted in unusually dry soil conditions and an increased sensitivity to drought.

Excessive spring moisture negatively affected red spruce growth at Roan Mountain. Negative relationships between radial growth and precipitation occur less frequently than positive relationships, but they are not unusual in sites where there is excess seasonal moisture, such as nearby Grandfather Mountain (Soulé, 2011). Excessive moisture can reduce growth through a reduction in the soil oxygen level, which subsequently inhibits root development (Fritts, 1976). At Roan Mountain, melting winter snowpack provides moisture in the early growing season and orographic enhancement of convective and frontal precipitation supplies moisture during summer months. The combination of a late melting of a large winter snowpack and a moist spring would result in a difficult growing season for red spruce trees. Additionally, a high amount of rainy spring days could result in reduced early season sunlight which would reduce net photosynthesis.

Moving analysis of the link between red spruce radial growth, precipitation, and PDSI further demonstrated that moisture availability (or overabundance) is less important than temperature conditions (Fig. 5). Significant negative relationships between growth and precipitation and PDSI during May of the current season were relatively brief and discontinuous. The most interesting moisture-growth correlation was a direct relationship during the 1990s and 2000s. This finding may represent an ongoing trend of red spruce shifting its sensitivity to water availability. During these decades, the drier conditions that were once favorable to growth seemed to become detrimental to growth. The co-occurrence of this trend with the weakening previous summer temperature signal during the 1990s and 2000s suggests that recent climate changes may have altered the relationship between red spruce growth and climate.

We observed a general decline in red spruce growth beginning around 1960 and lasting until approximately 1990 (Fig. 2). This decline may be related to acidic deposition, a hypothesis that much research of red spruce decline is in support of (Johnson and Siccama, 1983; Johnson, 1989; Mohnen, 1990; Eagar and Adams, 1992; Soulé, 2011). We also found a weakening trend in the previous-summer negative temperature growth relationship beginning in the mid 1990s, which could be related to reduced acid deposition levels and improving soil quality resulting from the pollution controls enacted by the Clean Air Act (EPA, 2012).

Conclusions

Our results suggest that a shift in climatic sensitivity occurred in the post-logging era. Similar mid-20th century shifts in red spruce sensitivity have been observed elsewhere (Cook et al., 1987; Johnson et al., 1988) with suspected linkages to changing climatic conditions (Cook and Johnson, 1989). In the post-logging era, the previous summer negative temperature growth relationship was the strongest and most temporally stable relationship, remaining significant until the present. The shifting nature of the red spruce climate–growth relationship was most likely a result of changes in disturbance regime. The notable shift in red spruce temperature-sensitivity coincided with the major stand composition and canopy structure changes that resulted from the 1930s logging activities. Spruce trees that survived the logging era experienced an open canopy directly after logging followed by a rapidly closing canopy from increasing density of Fraser fir (White et al., 2012). This series of abrupt changes may have resulted in a change in how red spruce responded to climate. However, we could not attribute such a shift in sensitivity solely to disturbance, as past researchers have attributed shifts in red spruce sensitivity in forests with less disturbed histories to climate change (Johnson et al., 1988; Cook and Johnson, 1989; Smith et al., 1999), and acidic deposition or other exogenous factors could complicate the climatic signal for radial tree growth. We conclude that an interaction of climatic influences and forest disturbance were the primary driving forces for the observed red spruce climate sensitivity shifts and fluctuations in signal strengths.

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