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# Evaluating the Influence of Disturbance and Climate on Red Spruce (Picea rubens Sarg.) Community Dynamics at its Southern Range Margin

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EVALUATION THE INFLUENCE OF DISTURBANCE AND CLIMATE ON RED
SPRUCE (*PICEA RUBENS* SARG.) COMMUNITY DYNAMICS AT ITS SOUTHERN
RANGE MARGIN

A Thesis Presented

By

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**ABSTRACT**

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Red spruce (*Picearubens)* populations experienced a synchronous rangewide decline in growth and vigor starting in the 1960's, which was likely caused by climate change or environmental disturbances (e.g., acid deposition); However, it is yet unknown if populations continue to decline or have recovered. In the context of global warming, red spruce is a species of concern because it is at its southern continuous range margin in Massachusetts. This study uses tree-ring data coupled with population data from permanent plotsto quantify the status of red spruce in Massachusetts. Tree cores were extracted from red spruce and used to examine radial growth rates, determine a growth-climate relationship, and document disturbance events. Red spruce at these plots ranged from 90 to 184 years old, and comprised 15 to 29 $m^2$/ha basal area. Over the past 50 years, red spruce has decreased in density, basal area, and relative importance while red maple, yellow birch, and American beech have increased. Red spruce saplings persisted in some plots, but the sapling layer was comprised mostly of American beech or red maple. However, red spruce seedlings were common at red spruce dominant plots

indicating that if favorable conditions occur, it could return to its more dominant position in the canopy.

Dendroclimatological analyses show that red spruce is sensitive to both temperature and precipitation. Most sites are correlated with temperature, while only two forests were correlated to precipitation. The general temperature response of the red spruce studied was positively correlated with winter temperatures while the general precipitation response was negatively correlated with precipitation. Temporal analysis of the climate-growth response indicates that red spruce here havenot had a temporally-stable, climate-growth relationship. Prior to 1960, radial growth was positively correlated with temperatures from November of the previous growing season to January of the current year. After 1960,all sites showed a shift in growth responses consistent with increased summer temperature stress; narrowed tree rings were formed during warm temperatures in July and August. Precipitation remained relatively constant over the past century, while temperatures have increased up to 2˚C across the study area. Of the two precipitation-sensitive forests, one forest shifted from being positively correlated with current January precipitation to negatively correlated with previous October precipitation while the second forest showed a strong positive relationship with August precipitation.

Because the radial growth of red spruce here are mostly constrained by temperatures, there has been negative growth response to regional warming and precipitation has been stable. I suggest the change in climate response is potentially due to warming and a physiological threshold response to increasing temperatures. Interestingly, disturbance frequency and intensity have increased over the same time

period, which could be either a trigger or a response to the shift in the growth-climate relationship.

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# CHAPTER 1

# INTRODUCTION

Climate change is altering forested landscapes across the northeastern United States (Loarie et al. 2009; Mohan, Cox, and Iverson 2009). Climate change can profoundly alter forest ecosystems, including phenological shifts leading to the decoupling of pollinator-plant relationships (Inouye and McGuire 1991), migration of species to maintain viable populations within specific-climate envelopes (Petit et al. 2008), and altered seed production and regeneration rates (Mohan, Clark, and Schlesinger 2004). In New England, annual temperatures have risen an average of $+0.08 \pm 0.01°C$ per decade over the last century, and $+0.25 \pm 0.01°C$ per decade for the past three decades (Hayhoe et al. 2006). The greatest changes over the last 35 years have been in winter, with almost a degree C per decade increase (Hayhoe et al. 2006).

Tree species at their southern range margins are likely to experience heat stress and exhibit reduced growth, with boreal species at southern limits most at risk because they are already living at the edge of their environmental tolerance (Easterling et al. 2007). Evidence of vegetation communities migrating to higher elevations over the past 40 years has already been observed (Beckage et al. 2008). Decreased habitat suitability at southern latitudes, resulting from direct and indirect anthropogenic influences (e.g., non-sustainable forestry practices and climate change) mightcause species to migrate north as climate becomes less favorable for their ideal growing conditions (Allen et al. 2010).

Massachusetts' Natural Heritage and Endangered Species Program lists spruce-fir forests as the most threatened by climate change, making these populations a high

research priority(MA NHESP 2010). Red spruce in Massachusetts is located primarily in the higher elevation forests of the Berkshire Mountains, in the northwestern corner of the state (Burns and Honkala 1990; Figure 1). Red spruce(*Picearubens*Sarg.*)* may be especially susceptible to climate change in Massachusetts because populations are isolated geographically. Red spruce populationsmay not have the topographic luxury to migrate north or higher up in elevation to escape a warmer climate, which could lead to a range contraction for spruce (Morin et al. 2008). Conversely, species such as tulip poplar (*Liriodendrontulipifera)*or pin oak(*Quercuspalustris)*,at their northern range limit in Massachusetts,may enjoy enhanced growth if climate continues to warm.

Red spruce (*Picearubens)* was extensively studied in the 1980's because of an observed widespread decline in vigor (Hornbeck and Smith 1985; Reams and Van Deusen 1993). Additional studies were also conducted to evaluate altered population dynamics and health throughout New England (Siccama 1974;Siccama, Bliss, and Vogelmann 1982; Battles, Johnson, and Siccama 1992; Battles et al. 2003; Webb et al. 1993) and in disparate populations in the Southern Appalachians (Cogbill and White 1988; Adams et al. 1985; Silver et al. 1991). Through dendrochronology, or tree-ring analysis (Fritts 1976;Fritts and Swetnam 1989; Johnson et al. 1988),researchers have investigated the decline of red spruce in the 1980's. A widespread decrease in radial growth measurements was documented throughout red spruce's northern range using tree ring analysis (Cook et al. 1987;Siccama, Bliss, and Vogelmann 1982),and in isolated populations in the southern Appalachians (Hamburg and Cogbill 1988) where researchers examined the environmental and climate sensitivity of red spruce.

Two popular hypotheses for the decline were proposed: a) stand history factors (e.g. pests, disturbance events) (Johnson and Siccama 1984; Conkey 1986, 1988; Van Deusen 1990; Vann, Strimbeck and Johnson 1992; Johnson et al. 1994; Boyce et al. 1991,2003; Battles et al. 2003; Webster et al. 2004; Lazarus et al. 2006;Beckage et al. 2008) and b) climate change factors (Siccama, Bliss and Vogelmann 1982; Scott et al. 1984; McLaughlin et al. 1987; Hamburg and Cogbill 1988; Johnson, Cook, and Siccama 1988; Van Deusen 1990; Cook and Cole 1991).Investigators of the stand history hypothesis argued that natural stand aging processes were responsible for the apparent decline of spruce at low-elevations, as they approached old-growth forest status, increased in age,or responded to local disturbance events (Conkey 1988, 1986; Van Deusen 1990). Investigatorsof the climate change hypothesis demonstratedthat the widespread radial growth(across elevations) was negatively correlated with increased winter and summer maximum temperatures and, more specifically, August temperatures (Cook et al. 1987), Ultimately scientists concluded that multiple factors and driving forces (including climate and stand-level disturbance events) lead to the widespread decline of red spruce observed in many high-elevation populations(Van Deusen, Reams, and Cook 1991). While this decline seemedfairly ubiquitous in red spruce populations, it is unknown if red spruce populations are still declining or have recovered from the 1960's decline (Gavin, Beckage, and Osborne 2008, Lazarus et al. 2006).

This study uses red spruce tree-ringdata coupled with population dynamics documented in continuous forest inventory (CFI) plots over the past 100 years, to provide a more comprehensive understanding of the status of low-elevation  (500-700 m. a.s.l.) red spruce in western Massachusetts. Tree-ring data were used to investigate the impact

of climate change on spruce growth rates at their southern continuous range margin.This will be accomplished with the following objectives: **1)**Use a series of field sites containing permanent plots from which to examine long-term population dynamics of red spruce at their lower range margin;**2)**Examine red spruce climate sensitivity to precipitation and temperature; **3)**Reconstruct red spruce disturbance history at low elevation permanent plots, to determine if frequency and intensity of disturbance events can explain radial growth trends over the past 100 years.With this research I tested threehypotheses: **1.**Red spruce has declined over the last 100 years in Massachusetts, both in total basal area and in radial-growth rates. **2.** Red spruce growth rate is negatively correlated with mean maximum summer temperatures and positively correlated with mean minimum winter temperatures. 3) The decline in radial growth will primarily be in response to a changing climate, specifically, increased summer temperatures.

**<u>Methods</u>**

**Study Area**

Study sites were located in the Western Massachusetts Taconic Mountains and Berkshire Plateau region, including portions of four State Forests: Mount Greylock (MG), Savoy Mountain (SM), October Mountain (OM), and Middlefield Forest (MF) (Figure 1). These four spruce-dominated forests were selected because they contained 0.08 ha circular Continuous Forest Inventory (CFI) plots that were established in the 1960's to continually monitor the status of Massachusetts state forests (see below). Mount Greylock is a National Natural Landmark, and is the highest point in Berkshire County, MA at 1064 m a.s.l. (Scanu 1988).

The climate is characterized by cold winters (average -5$^{o}$C) and moderately warm summers (average 19$^{o}$C). Average annual rainfall is 109cm, 55% of which falls from April to September. Average seasonal snowfall is 180 cm. The Berkshire region is underlain by igneous and metamorphic rocks, especially gneiss and schist (Scanu 1988). Mount Greylock is mainly granite and limestone. Soils are largely rocky glacial tills, with sand and gravel deposits proximate to waterways (Motts and O'Brien 1981). The geologic origin and history of the region is well documented (Egler 1940). Plots at Mount Greylockare located at higher elevations (678-978 m a.s.l.) than the three other forests (540-724 m a.s.l.; Table 1), but are relatively low-elevation when compared with Appalachian, Adirondacks, and Green Mountains red spruce communities.

**Site selection**

Seventeen field plots were selected from a subset of 0.08 ha circular plots establishedevery 0.8 km within a square grid across all State Forest Lands in 1960. I selected plots located on upland sites and categorized as containing at least 50% spruce-fir or red spruce basal area at the time of the last forest survey in 2000. The 17 plots were relocated using a handheld GPS unit and plot boundaries were re-established for the vegetation inventory during May through September 2010.

**Vegetation characterization**

At each CFI plot, all overstory trees >12.7cm diameter at breast height (DBH; 1.37 m above ground) were measured and identified to species (CFI protocol). Efforts were made to relocate previously numbered or painted overstory trees within each plot, to match exact tree measurements with past inventories; however paint had worn off most trees within plots so individual tree diameter comparisons were not made. All saplings (5

to 12.7 cm DBH) within the plot were tallied and identified to species. In addition, percent cover of seedling, shrub, and herbaceous species was estimated in a 5-m radius subplot located in the plot center and the most common species are reported here. Dead spruce trees were tallied; however due to the loss of individual tree markers and painted numbers, direct mortality comparisons were not made. Total basal area, red spruce basal area, and red spruce density were calculated for each sampling period (1960, 1980, 2000, and 2010), using past CFI data. Importance values were calculated using basal area and density of each species at a given plot, and average values are reported here. Nomenclature follows Gleason and Cronquist 1991.

## Dendrochronological Methods

### Field data collection

All overstoryred spruce (>10 cm DBH) trees within each plot were cored at DBH with an increment borer.  When < 10 red spruce occurred within a plot, additional red spruce located outside the plot were cored until at least 10 cores were obtained from each site.  Two cores per tree were extracted to identify any locally absent rings and to provide a better estimation of whole-tree radial growth. A total of 225 individual trees and 550 cores were collected from within and outside of allplots. Due to core defects (missed pith, compression wood, etc.) only 412 cores were used for disturbance analysis. From this pool, a subset of 213 cores weresuccessfully cross-dated and used for climate analysis.

### Sample preparation and measurements

All cores were brought back to the laboratory, dried, mounted, and sanded using progressively finer sand paper, up to 600-grit. Each core was visually cross-dated within each tree first using the list method (Yamaguchi 1991). Then cores were compared

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amongst trees within each plot. Cores were then measured to 0.001mm precision using a Velmex measuring system (Velmex, East Bloomfield, NY, USA) connected to an Olympus SZ40 microscope. Ring-widths were then used to statistically verify the accurate dating of each core with Spearman's correlations (with a critical level of 0.3281), using COFECHA (Holmes 1983).

**Data Analysis**

After verification using COFECHA, red spruce chronologies were built for each forest using the program ARSTAN (Cook 1985). ARSTAN generates four types of chronologies from the raw ring-width files: an average ring-width, standard, residual, and ARSTAN chronology. The average chronology contains mean ring-width, without any detrending. Standard chronologies are the compilation of ring-widths that have been detrended, but without additional autoregressive standardization. Residual chronologies are compilations of ring-widths, with auto-correlation removed. ARSTAN chronologies are compilations of ring-widths with the removal of auto-correlation, which is then pooled and added back to the ring-widths (e.g., preserving exogenous, low-frequency information). For ARSTAN I used a window of 32 years, with 16 year overlaps over the common period of 1930-2009, with a variance stabilization of one-third the length of the longest core. Data was first detrended with a negative exponential curve thendetrended with a -2/3 smoothing spline, with interactive detrending used on individual cores when necessary (e.g. when growth trends appeared inflated by poorlyfitteddetrending curves). I used the residual chronologies from ARSTAN for climate analysis created for each forest.

Temperature had a much stronger influence on red spruce radial growth than precipitation over time (Figures 9-11), although this relationship was  not temporally stable. Response function analysis (RFA) is a multiple regression technique that uses principal components of monthly climate data to estimate indexed values of ring-widths, was used to examine how climate influenced radial growth (Fritts 1976). RFA for minimum and maximum temperature and precipitation (Figures 12-14) showed significant responses in radial growth to minimum and maximum monthly temperatures and precipitation.

DendroClim2002 moving interval analysis (or moving window analysis)was used to detect a regional climate signal using the residual chronologies from ARSTAN.The dominant long-term climate trends are then compared with the DendroClim2002 analysis. To track the climate response over time (Fritts 1976), chronologies were correlated against mean monthly maximum and minimum temperature and precipitation from the prior March to October of the current year, from 1896 to 2009. Climate data from the PRISM project (PRISM Climate Group 2010)were correlated with tree-ring widths using Dendroclim2002 (Biondi and Waikul 2004). DendroClim2002 was used to analyze the chronologies from the previous March to the current October months using a moving window of 40 years. Only significant correlation values are plotted in the DendroClim graphs, with green representing the background (non-significant), red as a significant positive relationship, and blue as a significant negative relationship.

Stand dynamics within each forest were also reconstructed by evaluating all cores separately for abrupt growth releases using the criteria established by Lorimer and Frelich (1989), who defined a "major sustained release" as an average growth increase $\geq$ 100%

lasting at least 15 yr relative to the previous 15 yr and a "moderate temporary release" as an average growth increase $\geq$ 50 % lasting 10-15yr relative to the previous 10-15 yr. In addition, abrupt growth decreases $\geq$ 50 % lasting 10 yr relative to the previous 10 yr were tallied for each canopy tree as an indication of canopy damage (cf. Foster 1988; Orwig et al. 2001;Lafon and Speer 2002). The use of 10- and 15-year windows within these release criteria removed the effects of short-term growth responses due to climatic events (e.g., drought) (Lorimer and Frelich 1989; Nowacki and Abrams 1997). Disturbance chronologies were constructed for each study area by tallying the number of release and damage events by decade (Lorimer and Frelich 1989). Disturbances counted within one core from a tree were not recorded on the paired core from that same tree (Coopenheaver et al. 2009).

## <u>Results</u>

### **Stand composition**

Total stem density without red sprucein thehighest elevation plots, the Mount Greylock (MG) plots,decreased from 344$\pm$61 stems/hain 1960 to 242$\pm$75 stems/ha in 2000. Total basal area for all tree species except red spruce decreased from 31.1 ($\pm$6.8)m$^2$/ha in 1960 to 12.8$\pm$2.4 m$^2$/ha by 2010 (Figure 3, Table 1).Red spruce densitydecreased from 149$\pm$15 stems/ha to 138$\pm$34 stems/ha from 1960 to 2010, while also exhibiting a decline in basal area from 14.6$\pm$3.5 m$^2$/ha to9.9$\pm$ 3.6 m$^2$/ha by 2010 (Figures 2-3). Red spruce mortality varied across MG, from zero mortality to a loss of 30 stems/ ha. Many sites still supported a healthy population of red spruce (as demonstrated with numerous red spruce seedlings and saplings within the plot), while other sites have shown a trend of decreasing importance values relative to other species which now

dominate these plots. Yellow birch *(Betulaalleghaniensis),* balsam fir *(Abiesbalsamea)*, red and sugar maple *(Acer rubrum, Acer saccharum)*american beech *(Fagusgrandifolia)*, and black cherry *(Prunusserotina)* were common associate overstoryspecies in MG forest (Table 2). A majority of the saplings at MG were *Picearubens,* followed by*Abiesbalsamea,* and *Acer pensylvanicum* (Table 2). The understory vegetation consisted mainly of hobblebush (*Viburnum alnifolium*), Canada mayflower (*Maianthemumcanadense)*, marginal woodfern (*Dryopterismarginalis)*, and blue-bead lily (*Clintonia borealis)* (data not shown).

Red spruce density in the October Mountain (OM) plots decreased from $272 \pm 27$ stems/ha in 1960 to $167\pm58$ stems/ha in 2010, while also exhibiting a minor increase in basal area from$10.7\pm2.3$ m$^2$/ha to $11.3\pm 3.1$ m$^2$/haby 2010 (Figures 2-3). Total stem density except for red spruce decreased slightly from $235\pm 100$ stems/ha in 1960 to $260\pm69$ stems/hain 2010.Total basal area for all tree species except for red spruce increased from $6.7\pm3.5$ m$^2$/ha in 1960 to $17.8\pm 6.4$ m$^2$/ha in2010 (Figure 3). Red spruce mortality varied across OM, from 35stems/ha to 165 stems/ ha, with some sites retaining a red spruce dominant community, and other sites now largely composed of American beech and red maple with only relict red spruce trees remaining.Eastern hemlock (*Tsugacanadensis),* red maple *(Acer rubrum),* and yellow birch *(Betulaallenghaniensis)* were common associate overstory tree species in OM forest (Table 2). A majority of the saplings at OM were *Fagusgrandifolia,* followed by *Pinusstrobus, Acer rubrum, Abiesbalsamea, and Picearubens* (Table 2). The understory vegetation consisted mainly of solomon's seal (*Polygonatumcommutatum),* Canada mayflower

(*Mainanthemumcanadense),* marginal and spinulose wood ferns (*Dryopterismarginalis, Dryopteriscarthusiana)*, and starflower (*Trientalis borealis* (data not shown)*.

Red spruce density in the Savoy Forest (SF) plots increased from 82$\pm$58 stems/ha in 1960 to 155$\pm$ 39 stems/ha in 2010, while also exhibiting a slight increase in basal area from 6.5$\pm$3.5 m$^2$/ha to 9.6$\pm$ 5.3 m$^2$/ha in 2010. Total stem density except red sprucedecreased from 379$\pm$107 stems/ha in 1960 to 271$\pm$85 stems/ha in 2010 (Figure 2).Total basal area for all tree species except red spruce increased from 10.1$\pm$3.9 m$^2$/ha in 1960 to 13.8$\pm$2.7 m$^2$/hain 2010(Figure 3).Red spruce mortality ranged from a loss of 10 stems/ha to 60 stems/ha. Red maple (*Acer rubrum*), yellow birch (*Betulaalleghaniensis)*, and eastern hemlock (*Tsugacanadensis)*exhibited increased relative importance over time and were common associated species in the overstory of SF (Table 2). A majority of the saplings at SF were *Abiesbalsamea, then Fagusgrandifolia,* followed *Picearubens, Acer pensylvanicum, and Betulaalleghaniensis* (Table 2). The understory vegetation consisted mainly of balsam fir (*Abiesbalsamea)* seedlings, marginal and spinulose wood ferns (*Dryopterismarginalis, Dryopteriscarthusiana)*, and starflower (*Trientalis borealis)*(data not shown).

Middlefield Forest (MF) had a red spruce density of 791 stems/ha in 2000 and 111 stems/ha in 2010, with a basal area of red spruce at 27m$^2$/ha in 2000 and 0.2 m$^2$/hain 2010. Total stem density of all tree species except red spruce was 238 stems/ha in 2000 and 420 stems/ha in 2010.Total basal area of all tree species except red sprucewas 23.8 m$^2$/ha in 2000 and 13.3 m$^2$/hain 2010 (Figures 2-3). Red spruce was the dominant overstory species, with red maple (*Acer rubrum)* and eastern hemlock (*Tsugacanadensis)*the next most abundant associate overstory species (Table 2).Red

spruce decreased in relative importance from 72% in 2000 to 15% in 2010, while red

maple increased from 13% to 33%, and hemlock from 9% to 29%.There was a low

abundance of saplings within MF. The understory vegetation was largely goldthread

(*Coptistrifolia*), cinnamon fern (*Osmundacinnamomea*), and mountain laurel (*Kalmia*

*latifolia)* (data not shown).

**Dendrochronology**

Raw ring-width chronologies for each forest are shown in the (Figure 4), and

show a trend of declining radial growth rates over time. Trees growth rates naturally

decrease as they age, so this allometric trend of declining radial growth is expected. The

removal of these age-related growth trends through detrending, enables the distinction of

radial growth trends unrelated to age, suggesting an external force (such as climate or

environmental disturbance) are limiting tree growth. The residual chronologies (Figure

5)show only the potential influence of climate on tree-ring growth, without the additive

pooled data that the ARSTAN chronology contains, and presents a more conservative

response to climate parameters compared with the ARSTAN chronology. The ARSTAN

chronologies (Appendix Figure 16) showed the same patterns as the residual

chronologies, but with more pronounced peaks and valleys in the chronology.

Maximum temperatures were compared across each forest, and a general trend of

increasing temperatures of +1˚C annuallywas observed at MG, MF, and OM, while SF

remained relatively stable (Figure 6). Minimum temperature, on the other hand, shows an

increasing trend over the past century across all forests (Figure 7). Precipitation did not

show a trend of generally increasing over the past century, and remained relatively stable,

except for a prolonged decrease in total precipitation during a drought in the 1960's (Figure 8). MG, OM, SF, and MF residual and ARSTAN chronologies showed similar climate responses in Dendroclim, but only correlations with the residual chronology are presented here (Figure 5).

DendroClim moving interval analysis (using a moving 40 year window) with the MG residual chronology showed a consistent positive correlation between maximum and minimum temperatures from November of the previous year to February of the current growing year,from the late 1940s until 1986 (Figures 9-10). After 1986, MG radial growth is negatively correlatedto maximum and minimum temperatures in July (Figures9-10).Until 1960, MG growth was positively correlated with January precipitation (Figure 11), and beginning in 1976 we see a strong negatively correlation with October precipitation from the previous year.

The OM residual chronology had strong positive correlations with maximum and minimum temperatures from November of the previous growing season to February of the current year, which disappeared after 1986 (Figures 9-10). By 1966 however, an increasingly significant trend is observed with a negative correlation between growth and prior March maximum and minimum temperatures (Figures 9-10). No strong correlationsexist between precipitation and radial growth at OM for more than a few years (Figure 11).

The SF residual chronology shows a positive relationship between radial growth and maximum temperatures in December of the previous growing season and February of the current year, which are consistent until 1981 (Figure 9). A strong negative correlation between growth and July maximum temperatures of the current year is observed until

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1973, when it begins to deteriorate until 1985 when this relationship becomes insignificant.  By 1990 we instead see a strong negative correlation between growth and previous July maximum temperatures (Figure 9). Minimum temperatures from March of the previous growing season show a negative correlation with radial growth, which is consistent until the 1990's (Figure 10). February and September minimum temperatures from the current year show strong positive correlations with radial growth until 1985 and 2001, respectively. No strong correlations exist between radial growth and precipitation at SF for more than a few years (Figure 11), suggesting that precipitation was not the primary limiting factor influencing radial growth at SF.

MF exhibited weak correlations between growth and minimum and maximum temperatures, with no strong patterns emerging. The MF chronology showed a positive relationship between maximum temperatures from May until August of current growing season (Figure 9), from the late 1950s to mid 1970s. This relationship weakens after 1985, when growth is weakly negatively correlated with previous July maximum temperatures (Figure9). The MF residual chronology was positively correlated with minimum temperatures from April to October of the current growing season, which weakens in 1986 (Figure 10); however these correlations are weak compared with the strong patterns observed at the three other forests. Prior to 1960 for two decades, growth was positively correlated with previous March precipitation (Figure 11). After 1966, growth was positively correlated with previous September and current August precipitation.

**Disturbance History**

MG, OM, and SF had relatively similar patterns in disturbance history, while MF was largely undisturbed until the 1990's (Figure 15). Sites MG and OM exhibit a common disturbance pulse in the late 1930's/1940's, and MG, OM, and SF show a common pulse the 1960's-1980's (Figure 15). MG had a total of 87 minor disturbance events, 47 moderate disturbance events, and 104 growth decreases. OM had 51 minor disturbance events, 43 moderate disturbance events, and 112 growth decreases SF had 30 minor disturbance events, 16 moderate disturbance events, and 55 growth decreases. MF had 7 minor disturbance events, no major disturbance events, and 26 growth decreases. To compare between sites, the number of disturbances per tree were calculated, since there is an unequal sample depth across sites. MG had 1.088minor disturbances per tree, 0.5875 major disturbances per tree, and 1.30 growth decreases per tree. OM had 0.75minor disturbances per tree, 0.632 major disturbances per tree, and 1.647 growth decreases per tree. SF had 0.667minor disturbances per tree, 0.356 major disturbances per tree, and 1.23 growth decreases per tree. MF had 0.35 minor disturbances per tree and 1.3 growth decreases per tree.

At my sites, OM is the most heavily disturbed, with the greatest total number of major and minor disturbance events, and the greatest number of events per tree. MF exhibited very few disturbances relative to the three other sites. MG, OM, and SF all record an increasing number of disturbance events 30 years after the hurricane, consistent with the initiation of the widespread decline of red spruce. This increase in disturbances peaks in the1960's across MG, OM, and SF, and decreases in frequency until the 1990's. This suggests an initial pulse of disturbance in the 1960's, which begins to subside until the 1990's when across all four sites a spike in disturbance events is seen.

## Discussion

CFI data and tree-ring analysisdocument a decline in red spruce populationdensity, basal area,and radial growth across all forests and most sites.Despite mortality of older red spruce,some sites have shown a rebound since this decline, noted by red spruce regeneration recruiting into the tree size class. Several OM plots have shown this decline in red spruce, which may not be able to recover to a red spruce dominated forest, since the overstory is now a mix of northern hardwoods species, and the understory is dominated by shade-tolerant *Fagusgrandifolia* saplings and seedlings. Other sites have transitioned to an entirely new understory, while maintaining a red spruce dominated canopy (MF, SF); these sites also show very little red spruce regeneration (seedlings or saplings), which makes it less likelythat red spruce will persist as an important species at these sites. While some red spruce populations show a decline, other western Massachusetts red spruce populations (MG, several OM) appear "healthy", with red spruce still in the overstory and understory strata.This could be due to micro-climate insulation from increased temperatures, local adaptation to extreme environmental conditions, and genetic variation amongst these red spruce populations, among a variety of other reasons. Many studies on red spruce within the Northeast focus on winter injury and the long-term influences of consecutive winter injury years (Lazarus et al. 2006) or the decline of high-elevation spruce-fir forests (Battles et al. 2004), where this rebound trend is non-existent. Other studies from the southern Appalachians point to a similar rebound of red spruce (Moore, Van Miegroet, and Nicholas 2008). This rebound in the Appalachians may seem more apparent since balsam woolly adelgid

(*Adelgespiceae*) is decimating the co-dominant overstory species, Fraser fir

(*Abiesfraseri*).

The non-stable climate relationships observed at my sites can be explained by one

of two mechanisms: climate change, or a physiological tolerance/ threshold response and

follows the findings of Cook and Johnson (1989). A third option exists, which blends the

two mechanisms (climate change or tree physiology) into a single explanation (climate

change induces physiological changes within red spruce trees). While a consistent

climate-growth relationship is observed across sites during the first half of the twentieth

century, a distinct shift in this relationship is observed beginning in the 1960's, but is

variable across sites. This variability supports a climatic-threshold response as opposed to

acid deposition,since it is not synchronous across these sites. This supports the theory that

trees have shifted their growth patterns and carbon allocation (ring-widths) in response to

climate conditions on an individual basis. In contrast you would expect uniform response

to environmental pollution, across all sites, which I do not see here in Western

Massachusetts. Additional factors to be considered in future studies include soil

characteristics (depth, aspect, quality), and forest density. Other studies have shown

environmental pollution to play a significant role in shaping red spruce communities,

with a similar magnitude of response (Johnson et al. 1984, 1994; Webb 1993).

While acid deposition may have influenced these red spruce populations, I have

not specifically investigated it in this study.In New York and Vermont acid deposition

was considered to be more of a driving force for decline of red spruce, especially since

foliar and soil chemistry has been altered (Battles 2003, McLaughlin et al. 1987). In the

high elevation forests acid deposition is believed to exacerbate red spruce decline, and

with the introduction of the clean air act in 1970 a recovery of high-elevation red spruce populations would have been likely (Van Deusen 1990). At my sites, there were no visible signs of needle reddening or winter injury, however foliar and soil chemistry studies could provide insights into disruption in nutrient cycling and other aspects of these red spruce forests.

Prior to the 1960's I observed a positive growth response to warmer maximum winter temperatures (previous November to current February), and a similar positive response to minimum winter temperatures (previous November to current February) (Figures 10-12). After the 1960's, I observe a distinct shift to strong negative growth in response to maximum and minimum summer temperatures (July). This shift suggests that in the 1960's trees started being limited by the high summer temperatures, which were having detrimental effects on growth as shown by decreased annual ring-widths. Since we no longer observe the pre-1960 trend of positive growth correlating to winter temperatures, this also suggests that climate is having more of a detrimental influence on tree-growth throughout the growing season, not just during the hot summer months. These trends are similar to Cook et al. (1987) and McLaughlin et al. (1987), who observed late summer temperatures negatively influencing red spruce radial growth.

It is striking that precipitation was not strongly correlated with growth at most of these sites, after the 1960's. Specifically the 1960's drought represents a prominant intense climate event, and after that time precipitation was no longer a limiting factor at my sites, and increased precipitation correlated with decreased ring-widths. High-elevation forests tend to be more limited by temperature (Schweingruber 1996), and low-elevation sites are typically more sensitive to precipitation (Cook et al. 2004). Webb et al.

(1993) found that range-edge red spruce in bog sites were slower-growing and more robust populations, while upland sites suppoortedincresingly drought sensitive population. Similarly, my study sites display this increased drought sensitivity after the extensive drought of 1960.  MF did show a precipitation response, unique in comparison to the three other forests sampled. Prior to 1960 growth was positively correlated with precipitation from March of the previous year. After 1960, we see a pattern shifting in how trees respond to precipitation, similar to the pattern of temperature response which shifts in the 1960's. After 1960, MF began to have a strong positive correlation with precipitation from the previous September and August of the current growing season with radial growth in red spruce at MF. While MF was not the youngest forest, competition may have influenced population dynamics at this plot.

Climate change seems to be the primary driving forcefor growth changes in my study sites. The sudden shift in ring-widths in response to temperatures, suggest that temperature is the primary limiting factor at my sites. This shift from positive to negative growth correlations reinforces the hypothesis that the climate where these trees established has changed over the past 100 years, and is now warmer than ideal growing conditions for *Picearubens.*  We cannot ultimately conclude that climate change is the only causal agent, nor that it is the causal agent at these sites since the climate-growth relationship is not temporally stable. After developing a long chronology for Norway spruce, Büntgen et al. (2005)  founda similar lack of stability between the growth/climate relationshipsfor populations fromthe Alps. They suggest an increasing sensitivity to drought could be altering the climate/growth response for Norway spruce. This could translate to increased temperatures leading to increased evapotranspiration within the

trees. While I did not directly measure rates of evapotranspiration, drought-stress is a plausible explanation for declining radial growth of red spruce in Western Massachusetts forests-specifically induced by the 1960's drought. Prior to the 1960's drought red spruce at my sites show a positive response to precipitation, and after the drought show an increasingly negative correlation with precipitation.

There were clear patterns in red spruce growth across three forests in response to both maximum and minimum monthly temperatures. Tree-ring analysis indicates that the red spruce climate-growth relationship changed around 1960, synchronous with the radial growth declines seen in the raw and standardized chronologies. Prior to 1960 radial increment was consistently positively correlated with minimum and maximum monthly temperatures from November of the previous growing season to January of the current year at most sites. A shift in growth responses to climate parameters is consistent across all sites, although the timing is not synchronous across the forests. Trees begin responding negatively to maximum and minimum monthly temperatures in July and August at most sites after 1960.

The threshold response model (Cook and Johnson 1989) is supported by this data; there was a distinct shift in growth responses to climate, and variable points in time, which you wouldn't expect if an environmental pollutant was uniformly influencing these forests.  However, similar to a climate threshold, a pollution threshold may have exacerbated the changes in tree physiology during this time, compounding negative growth affects on these red spruce trees. This suggests that red spruce trees began to physiologically respond differently to climate after reaching a specific threshold, unique to their local environment and microclimate. *Picearubens* at my sites may have been

responding to climate positively prior to increasing temperatures in the 1960's, until

reaching a certain exposure to higher temperatures or other climatic factors when it

responded to climate differently. Since this pattern is observed at my highest elevation

sites (Mount Greylock) as well as my mid-elevation sites, we can conclude that climate

would be influencing each site at a different rate, but that a widespread shift occurred

over 20 years from 1960-1980 in Western Massachusetts.

The disturbance history gleaned from tree ring analysis provides information

about the number of growth release events, stand replacing events, and growth decreases.

These relative measures of growth increases and decreases by themselves tell us how

disturbed a given site is, and can be combined with known weather events, such as wind

storms, ice storms, and more catastrophic weather events to observe how trees respond to

given weather events. At MG, OM, and SF, I observed a pulse of minor and major

disturbance events in the 1930's, which is the decade of the 1938 Hurricane (Boose,

Foster and Fluet 1994; D'Amato and Orwig 2008). Interestingly, MF seems to have

beeninsulated from the 1930's pulse observed at the other three sites. When comparing

the four forests, I also observed that MG, OM, and SF show a common trend of

increasing growth declines in the 1960's through 1980's which corresponds to the time

when widespread red spruce decline was observed in the northeast(Figure 7). Climate

change may be playing a role in increasing the frequency and severity of disturbance and

extreme weather events (Smith 2011;Daniels et al. 2011; Frich et al. 2002; Easterling et

al. 2000; Vellinga and van Verseveld 2000).

**Conclusion**

21

Western Massachusetts red spruce forests are declining overall in density, basal area, and radial growth. Red spruce forests have shifted over time to new forest types, changing from red spruce or spruce-fir to predominantly northern hardwoods forests as demonstrated by the changes in basal area and density of red spruce at these sites. These forests still include red spruce, but where it is  not nearly as important as it was 50 years ago. Massachusetts populations are largely low-elevation (500-700 a.s.l.) in comparison to sites in the Adirondacks, Vermont, and Appalachian mountains. Additional studies in low-elevation red spruce populations will help to discern whether climate or physiology is mediating the red spruce growth decline observed in the 1960's-1980's. Some individual trees show a rebound in radial growth beginning in the 1990's, which is likely due to growth release events and decreased proximate competition with other trees, rather than a response to more favorable recent climate.  Massachusetts red spruce populations, examined in this study, show a continued radial growth decline since the 1960's based on the tree ring data, and since the recent climate has been less favorable for spruce, it is likely that decreased competition has led to increased growth rates in individual trees.

The two plausible reasons for the observed growth patterns are either a response to climate change and increased average summer and winter temperatures, or due to a physiological threshold which shifted how trees grow in response to climate (Wilmking et al. 2004, 2005, Driscoll et al. 2005, D'Arrigo et al. 2008) . Red spruce populations in this state have shifted how they respond to climate, beginning in the 1960's. This shift mightnot necessarily be the result ofdramatic climate change, or  a peak in environmental pollution at that time. Additionally, some sites show a decline in ring-widths from the 1960's to the 1980's but an increase in ring-widths in the 1990's, but then a recent drop

in ring-widths. This suggestsa recovery of the population, which is supported by the CFI

data and recruitment of new red spruce saplings into the tree size-class.  This would

suggest that several driving forces, including but not solely climate changes, are

responsible for the decline in red spruce growth. These Western Massachusetts red spruce

chronologies do not demonstrate a temporally stable climate-growth relationship, making

dendroclimatology studies with this species potentially challenging.
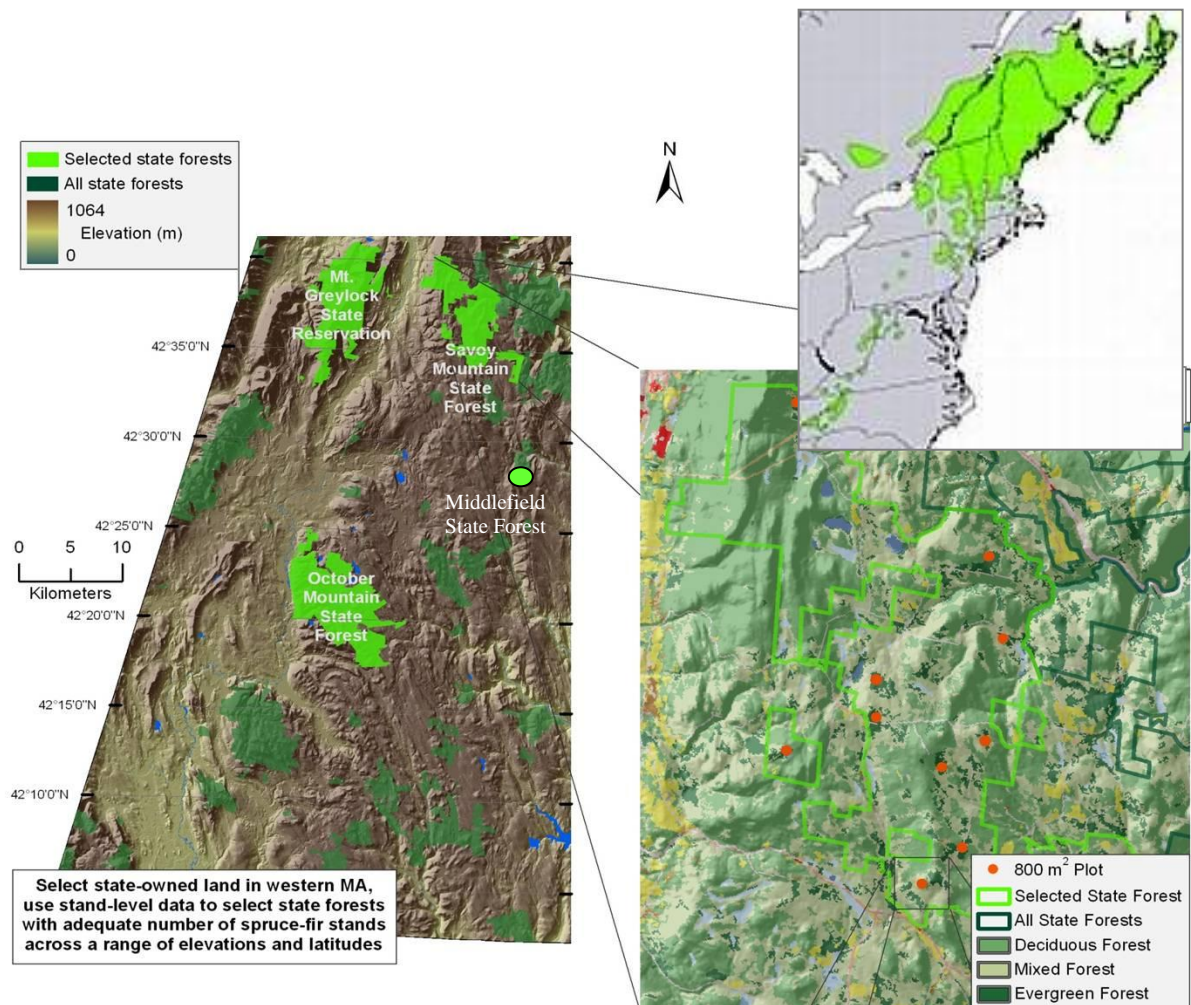


**Figure 1. Map of site locations, with key forests highlighted in green. Inset shows Savoy Forest, with red dots representing individual CFI plots distributed throughout that forest. Upper right panel shows the complete range of red spruce.**

**Table 1.Location (decimal degrees) at CFI field sites. Note the number of plots at each site.**

| | Mount Greylock | October Mountain | Savoy Forest | Middlefield Forest |
|---|---|---|---|---|
| Latitude | 42.622364 | 42.358235 | 42.594551 | 42.401972 |
| Longitude | -73.181151 | -73.1771771 | -73.0288963 | 73.0808754 |
| Elevation | 678-959 m | 540-613 m | 528-724 m | 542 m |
| Number of plots | 7 | 5 | 4 | 1 |

**Table 2. Species overstory relative importance values (relative density\*relative dominance)/2, and the most common sapling densities, and understory species percent cover in four *Picearubens* of Western Massachusetts.**

| Overstory  Species | MG 1960 IV (%) | MG 2010 IV (%) | OM 1960 IV (%) | OM 2010 IV (%) | SF 1960 IV (%) | SF 2010 IV (%) | MF 2000 IV (%) | MF 2010 IV (%) |
|---|---|---|---|---|---|---|---|---|
| *Abiesbalsamea* | 24.4 | 39.6 | 8.0 | 8.8 | 9.5 | 3.9 | 1.4 | 6.6 |
| *Acer rubrum* | 20.2 | 14.3 | 4.3 | 19.4 | 13.2 | 29.9 | 13.4 | 33.2 |
| *Acer saccharum* | 24.4 | 8.4 | - | - | 28.9 | 7.8 | - | - |
| *Betulaalleghaniensis* | 24.0 | 14.7 | 16.7 | 11.7 | 10.7 | 6.5 | 2.9 | 11.4 |
| *Betulapapyrifera* | 9.5 | 14.8 | 2.2 | 13.6 | 1.5 | 11.4 | 1.3 | 4.4 |
| *Fagusgrandifolia* | 4.1 | 9.9 | 2.5 | 3.3 | 13.2 | 37.1 | - | - |
| *Fraxinusamericana* | - | - | 2.9 | 2.6 | 6.4 | 11.7 | - | - |
| *Picearubens* | 33.0 | 39.8 | 69.4 | 38.5 | 37.4 | 34.8 | 72.0 | 15.2 |
| *Prunusserotina* | 5.5 | 14.7 | 14.4 | 10.0 | 4.5 | 8.2 | - | - |
| *Tsugacanadensis* | - | - | 14.1 | 30.4 | 14.3 | 26.6 | 8.9 | 29.3 |
| Other species | 8.2 | 2.9 | 11.1 | 11.8 | 1.6 | 2.6 | - | - |

| Saplings | Density/ha$^{-1}$ (MG) | Density/ha$^{-1}$ (OM) | Density/ha$^{-1}$ (SF) | Density/ha$^{-1}$ (MF) |
|---|---|---|---|---|
| *Abiesbalsamea* | 185.4 | 154.5 | 617.9 | 12.4 |
| *Acer pensylvanicum* | 119.5 | 12.4 | 185.4 | - |
| *Acer rubrum* | - | 185.4 | - | 49.4 |
| *Betulaalleghaniensis* | 49.4 | 129.8 | 80.3 | 37.1 |
| *Fagusgrandifolia* | 61.8 | 271.9 | 278.0 | - |
| *Ilex verticillata* | - | - | - | 74.1 |
| *Picearubens* | 262.0 | 143.4 | 216.3 | 74.1 |
| *Pinusstrobus* | - | 185.4 | - | - |
| *Tsugacanadensis* | - | 86.5 | - | - |

| Understory Species | % cover (MG) | % cover (OM) | % cover (SF) | % cover (MF) |
|---|---|---|---|---|
| *Dryopterismarginalis* | 19 | 6 | 6 | - |
| *Dryopterisspinulosa* | 5.6 | 9 | 12 | - |
| *Maianthemumcanadense* | 14.6 | 1.6 | 2 | - |
| *Osmundacinnamomea* | 4.6 | 0.4 | - | 45 |
| *Trientalis borealis* | 2.8 | 2 | 2 | - |
| *Viburnum alnifolium* | 9.4 | 3 | 1 | - |
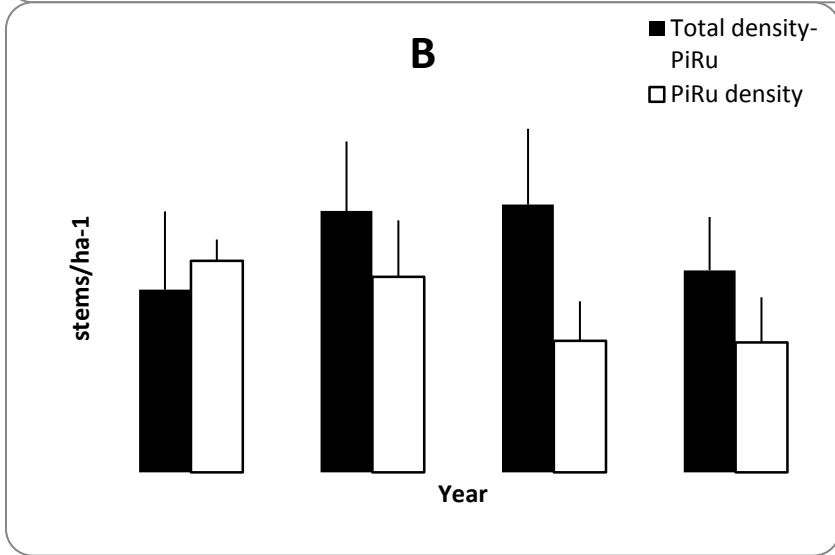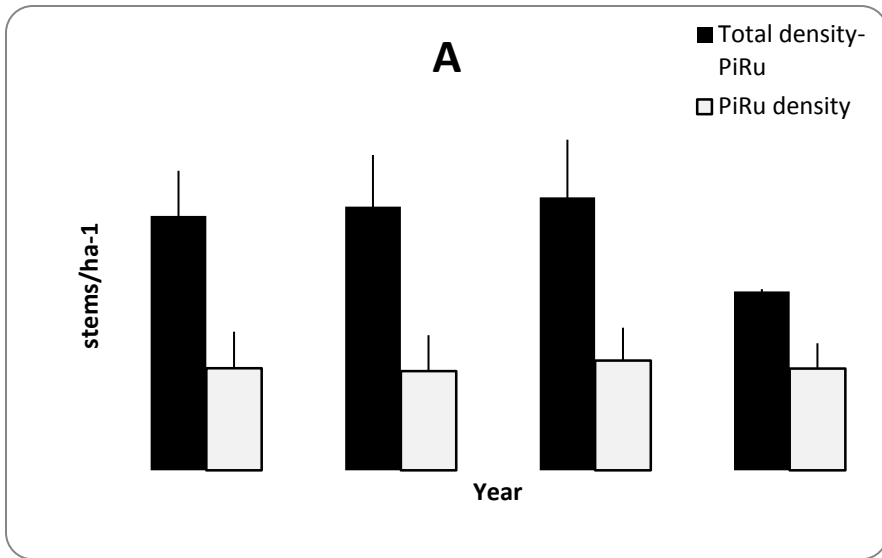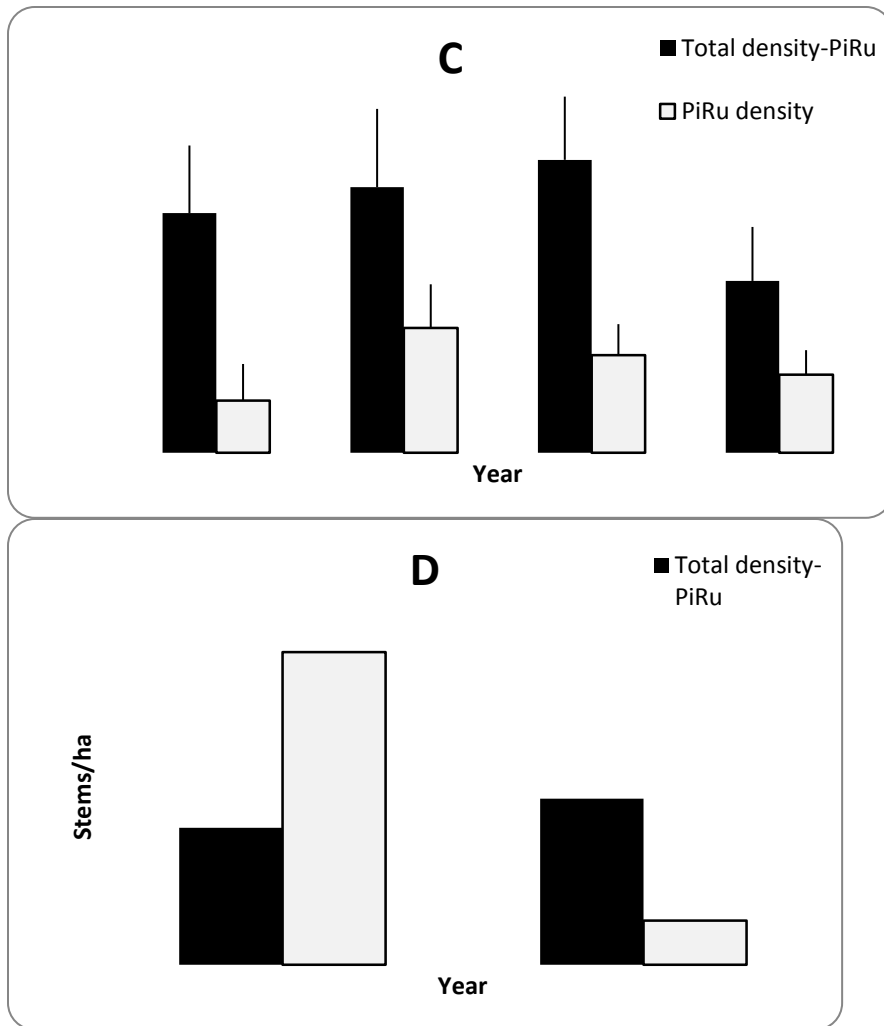
**Figure 2. Density of all overstory tree species total stems/ha$^{-1}$ and red spruce stems/ha$^{-1}$ in MG (A), OM (B), SF (C), and MF (D) forests over time.**
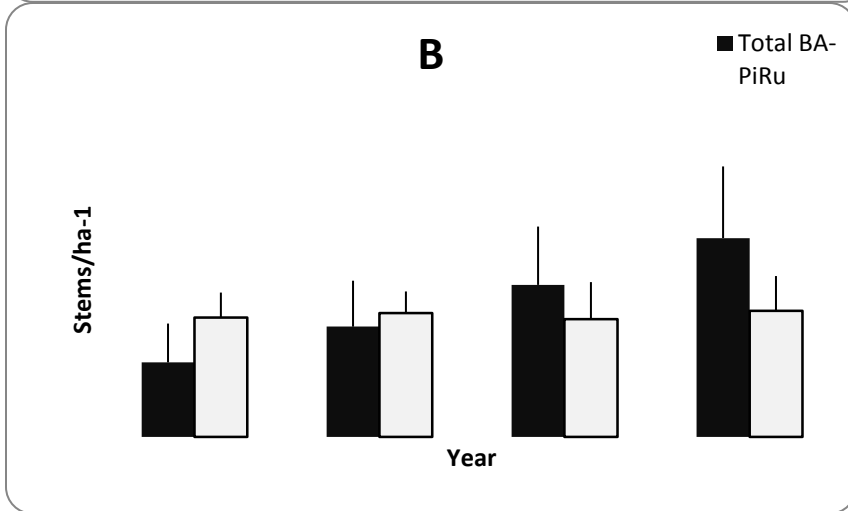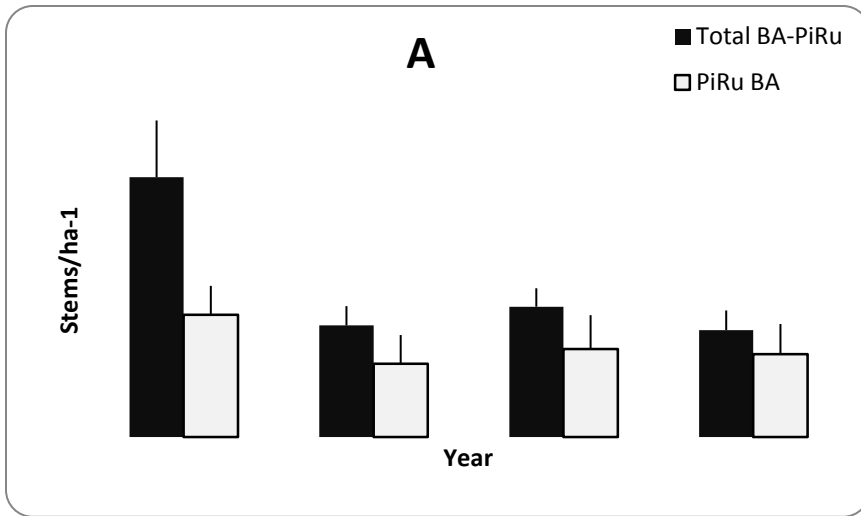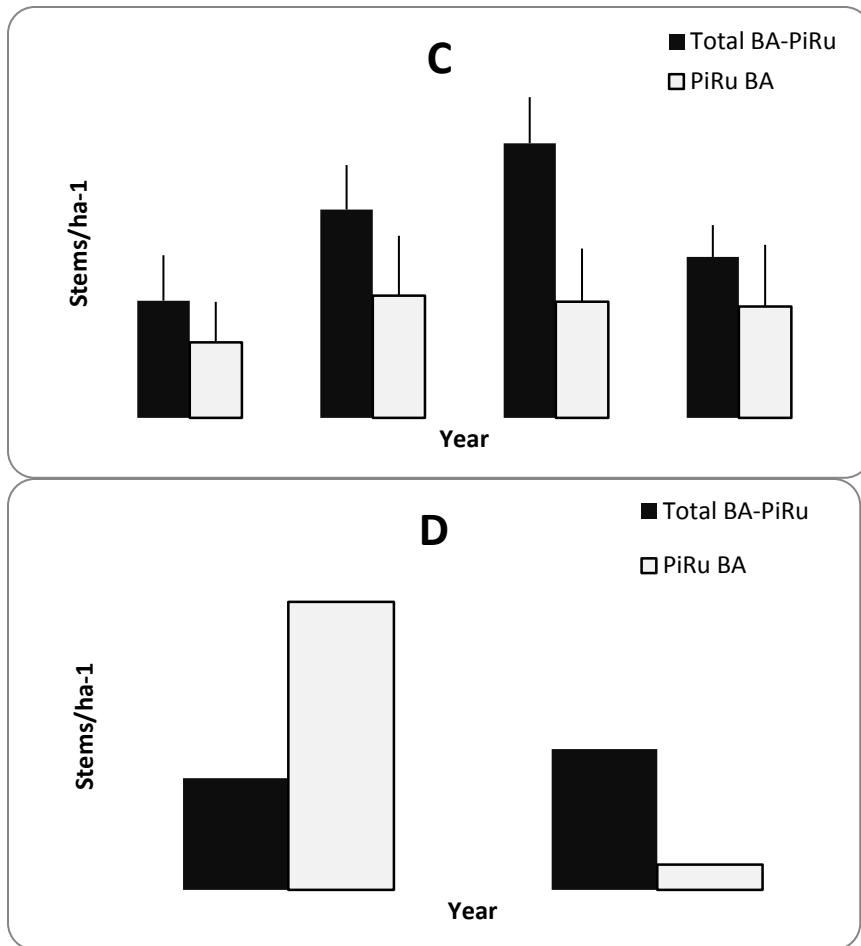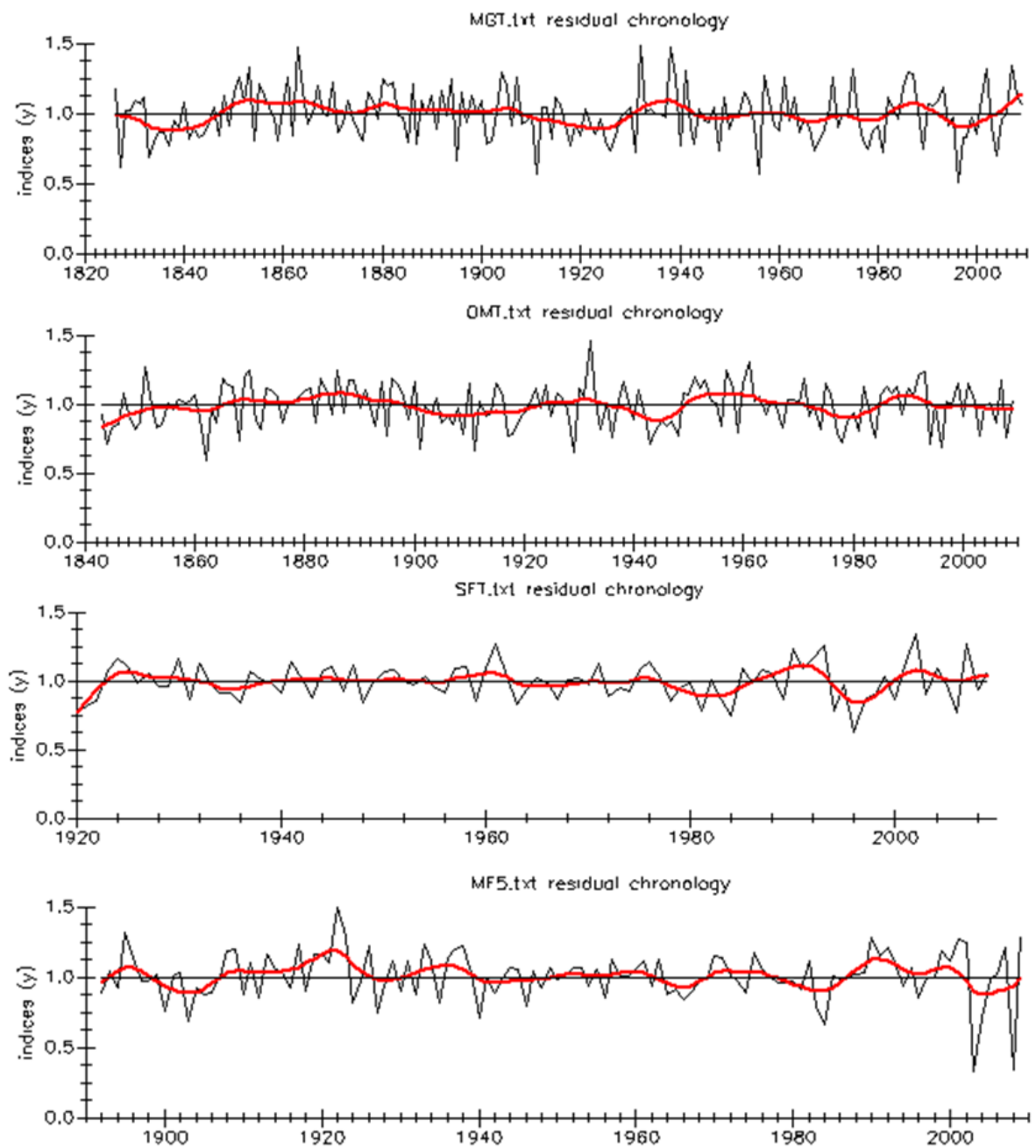
**Figure 3.**Basal area (m$^2$/ha$^{-1}$) of all overstory tree species (total) and red spruce in MG (A), OM (B), SF (C), and MF (D).
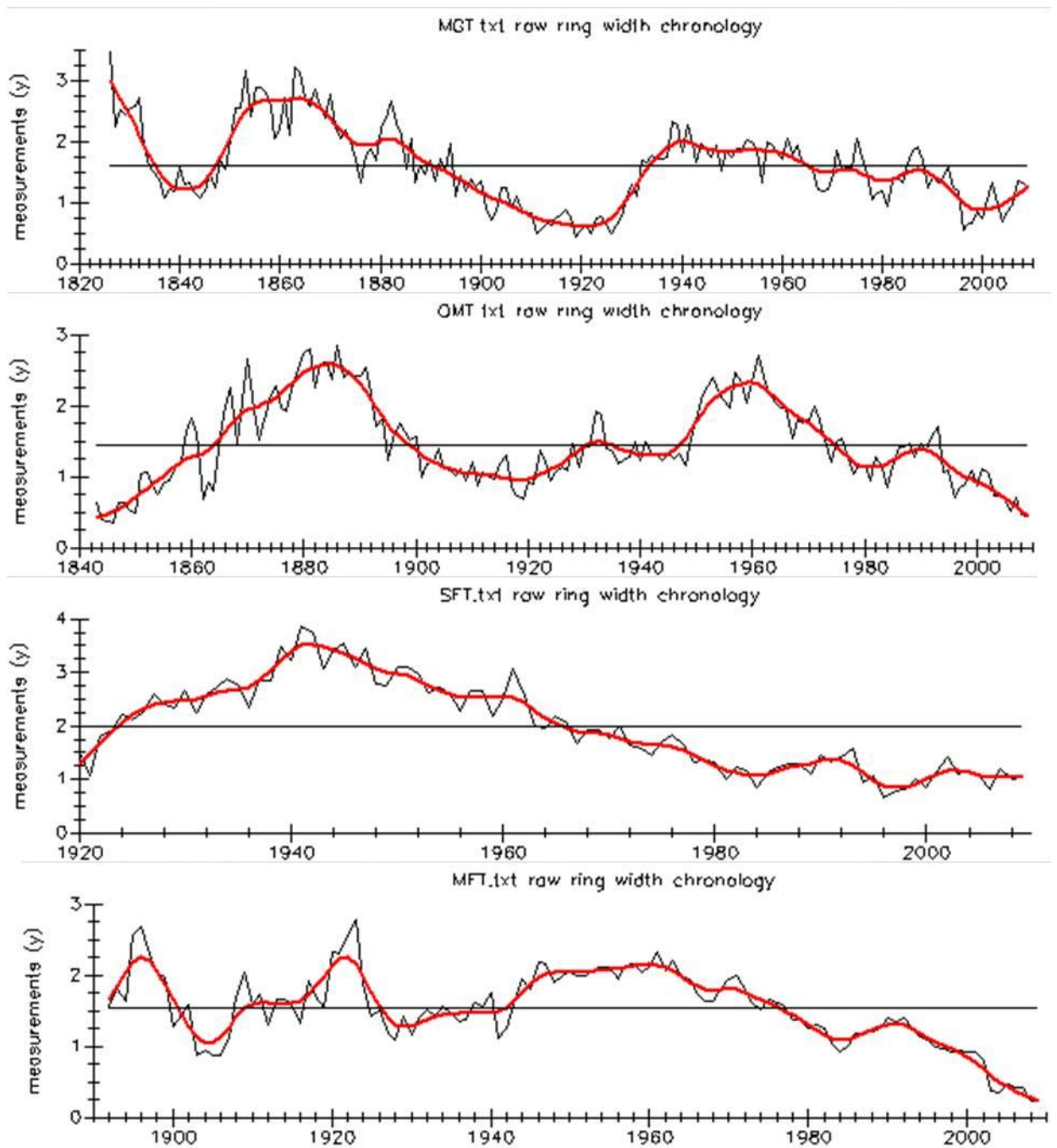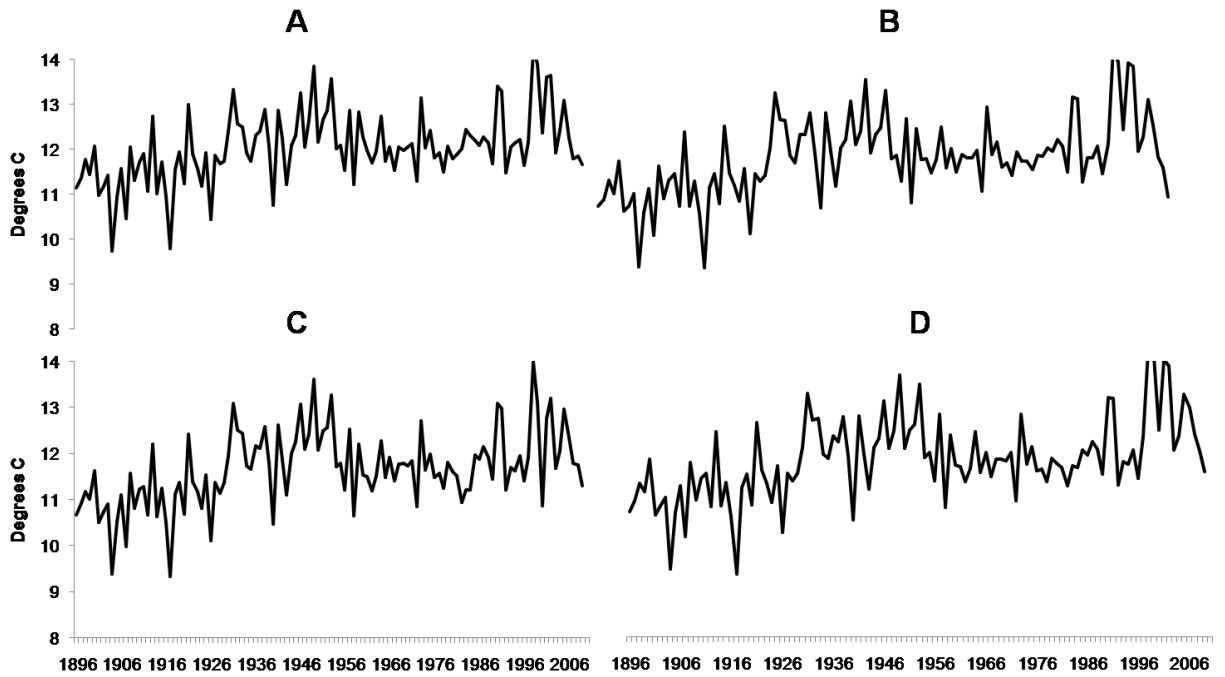
**Figure 4. Raw ring width chronologies for each forest, showing the general growth patterns before filtering/detrending, with a smoothing spline applied.**

**Figure 5. ARSTAN residual chronologies for each forest, showing average ring-widths at these sites over time, after detrending, with a smoothing spline applied.**

**Figure 6. PRISM data for each siteMG(A), OM(B), SF(C), and MF(D), showing mean maximum annual temperatures on the left axis, with a trend line showing increasing mean annual temperatures.**
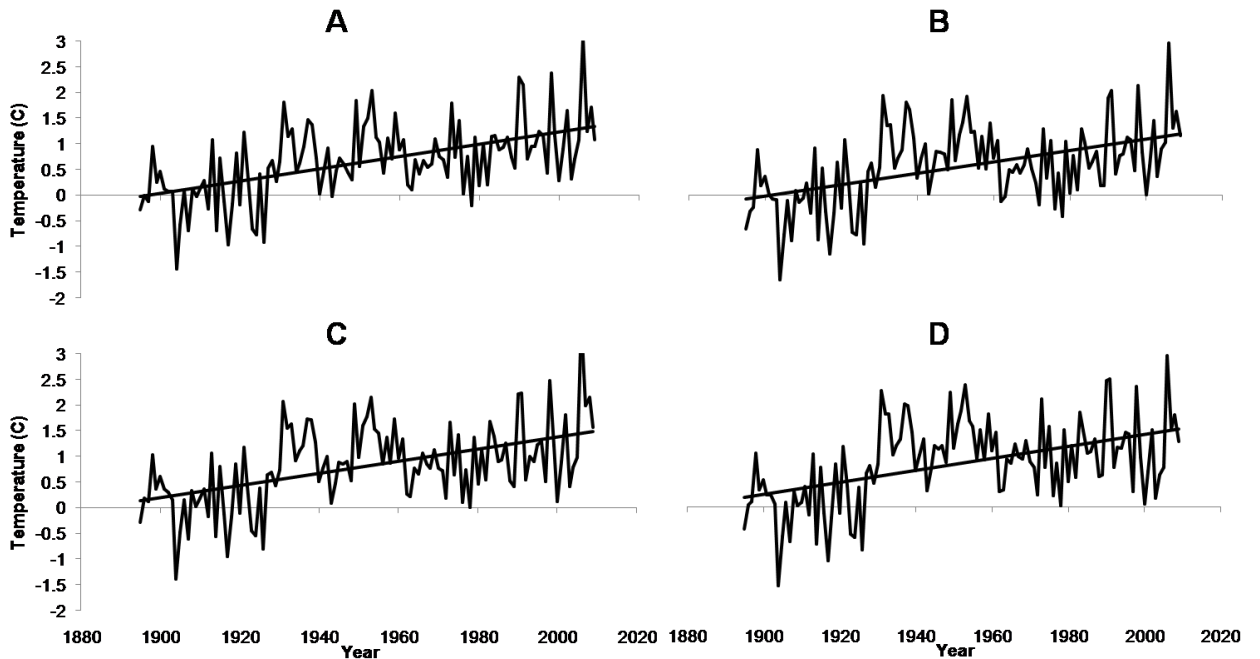


**Figure 7. PRISM data for each site, showing mean minimum annual temperatures on the left axis, with a trend line showing increasing mean temperatures.**
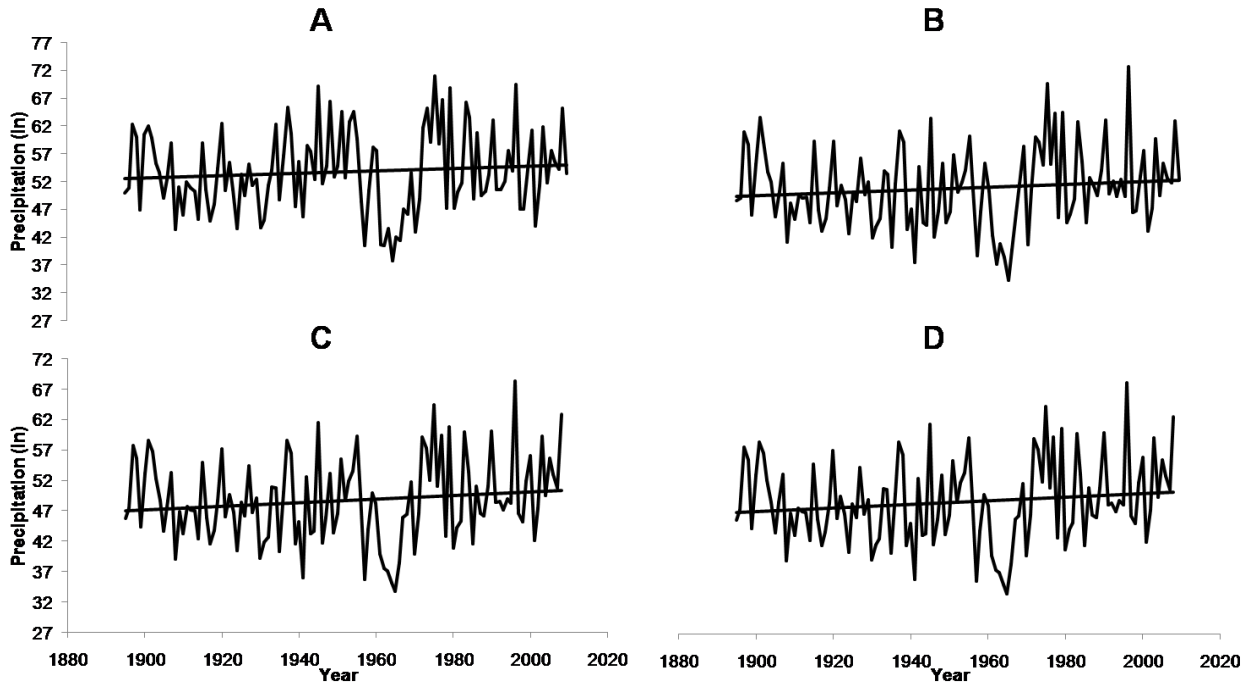
**Figure 8. PRISM data for each site, showing mean annual precipitation on the left axis in inches, with a trend line showing minor increases at SF (C) and MF (D).**
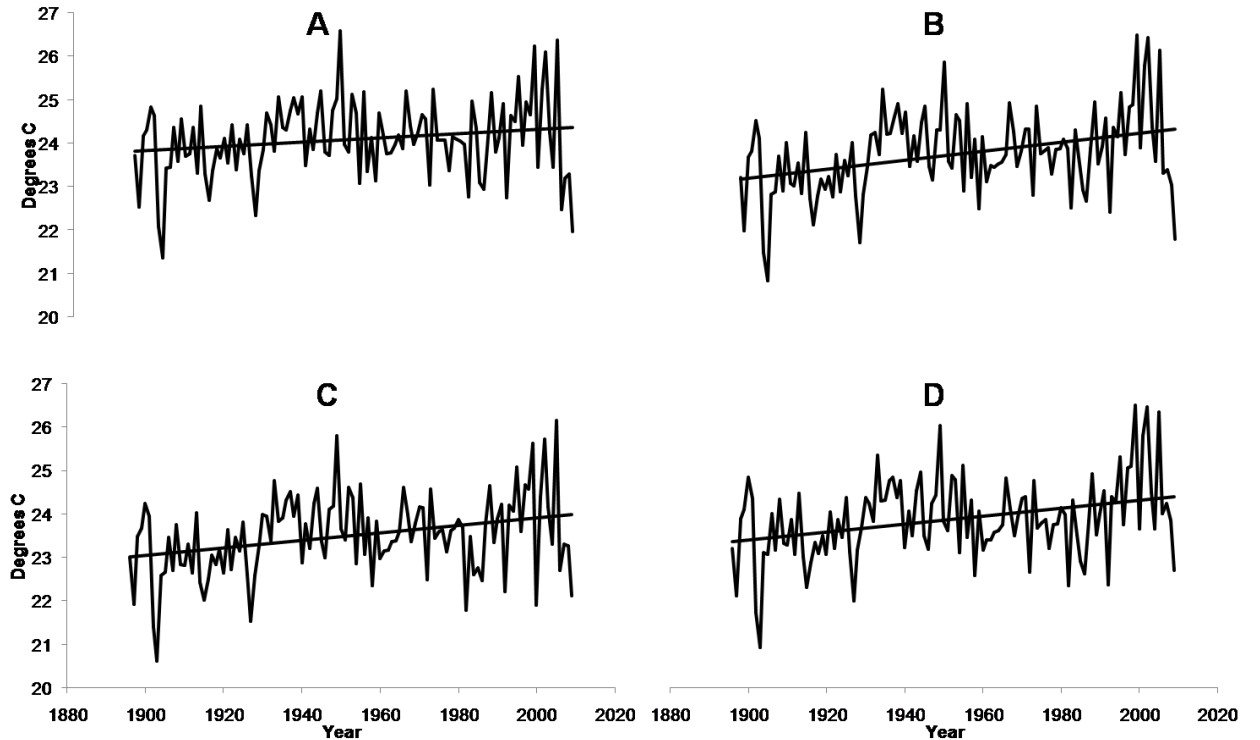


**Figure 9. PRISM data for each site, averaged over the summer months of June, July, and August.**
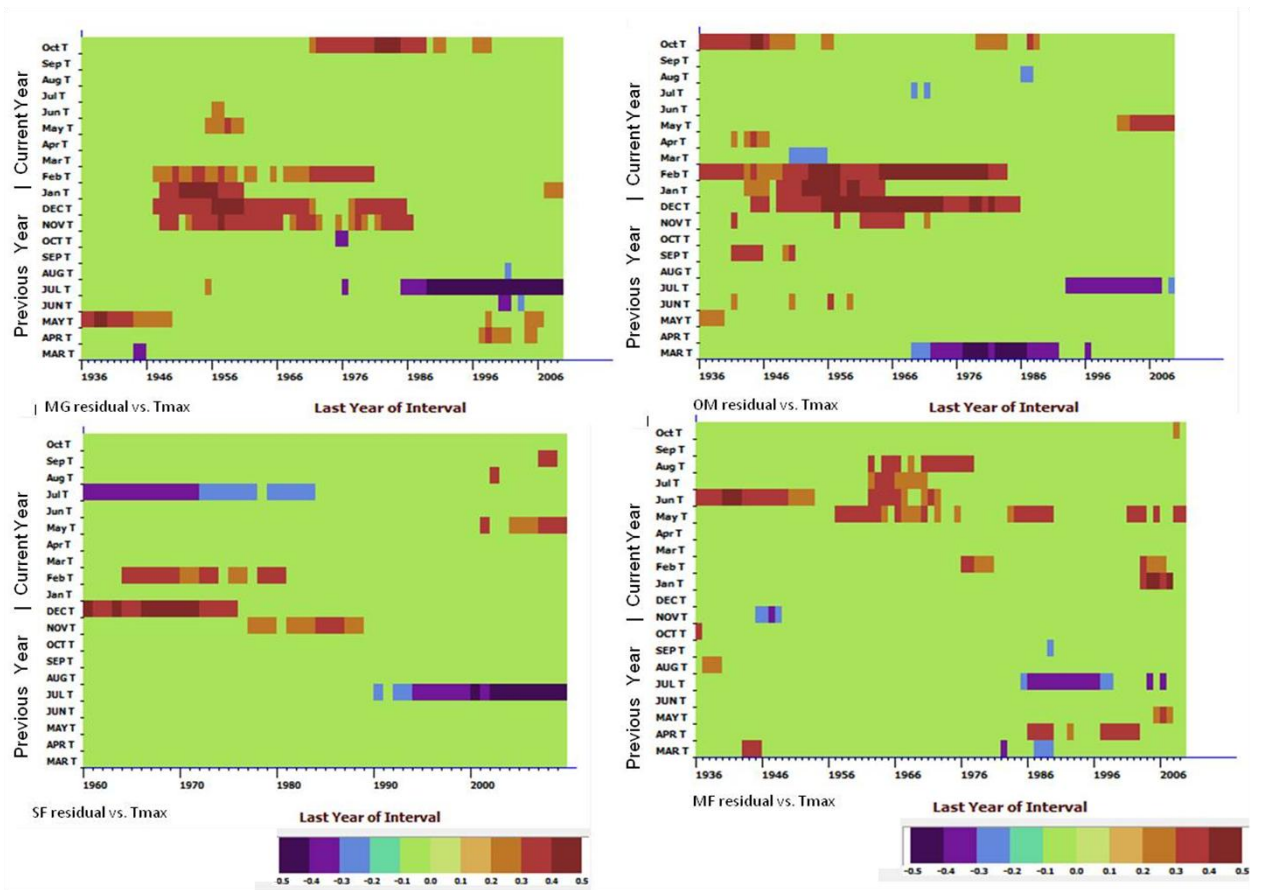
**Figure 10. Moving interval analysis graphs from DendroClim showing correlations between a site's residual chronology and maximum monthly temperatures for that site.**
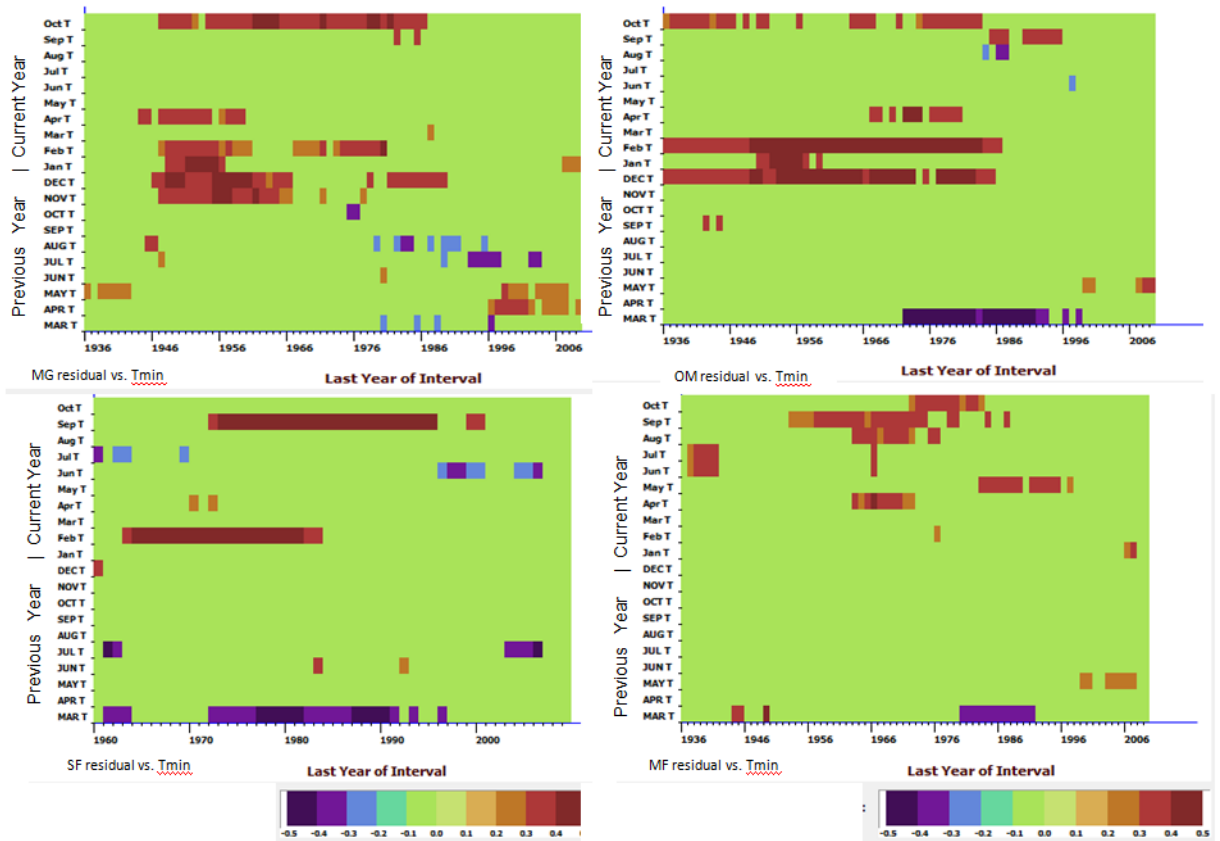
**Figure 11. Moving interval analysis graphs from DendroClim showing correlations between a site's residual chronology and minimum monthly temperatures for that site.**
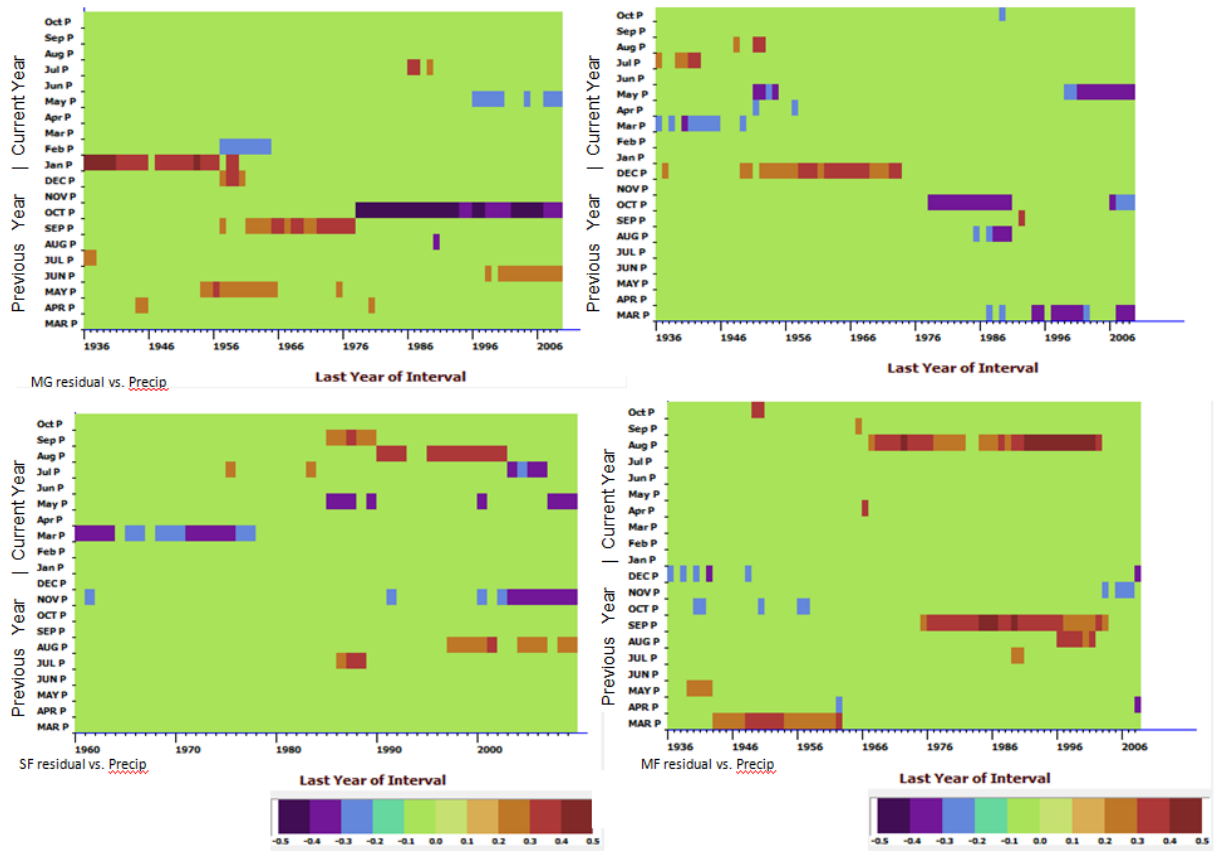
**Figure 12. Moving interval analysis graphs from DendroClim showing correlations between a site's residual chronology and monthly precipitation for that site.**
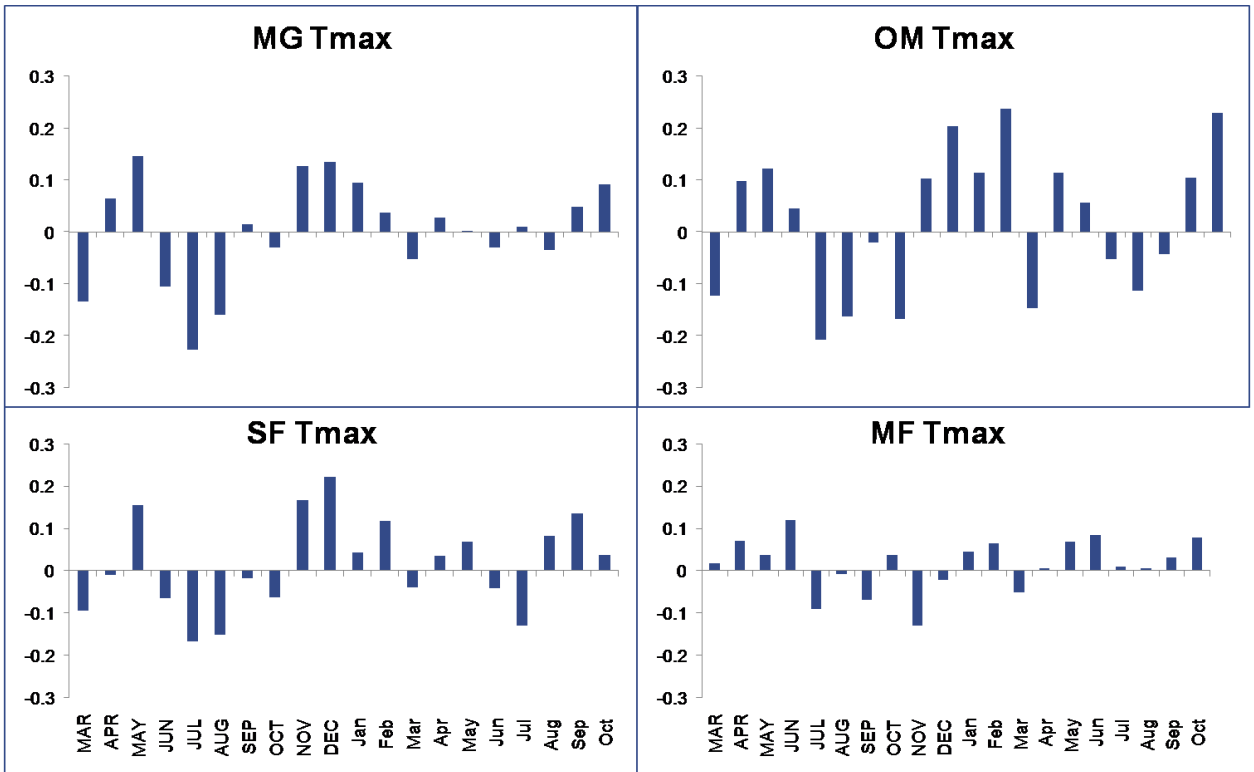
**Figure 13.** Correlations between maximum temperature and the residual chronology of *Picearubens* at four forests in Western Massachusetts.
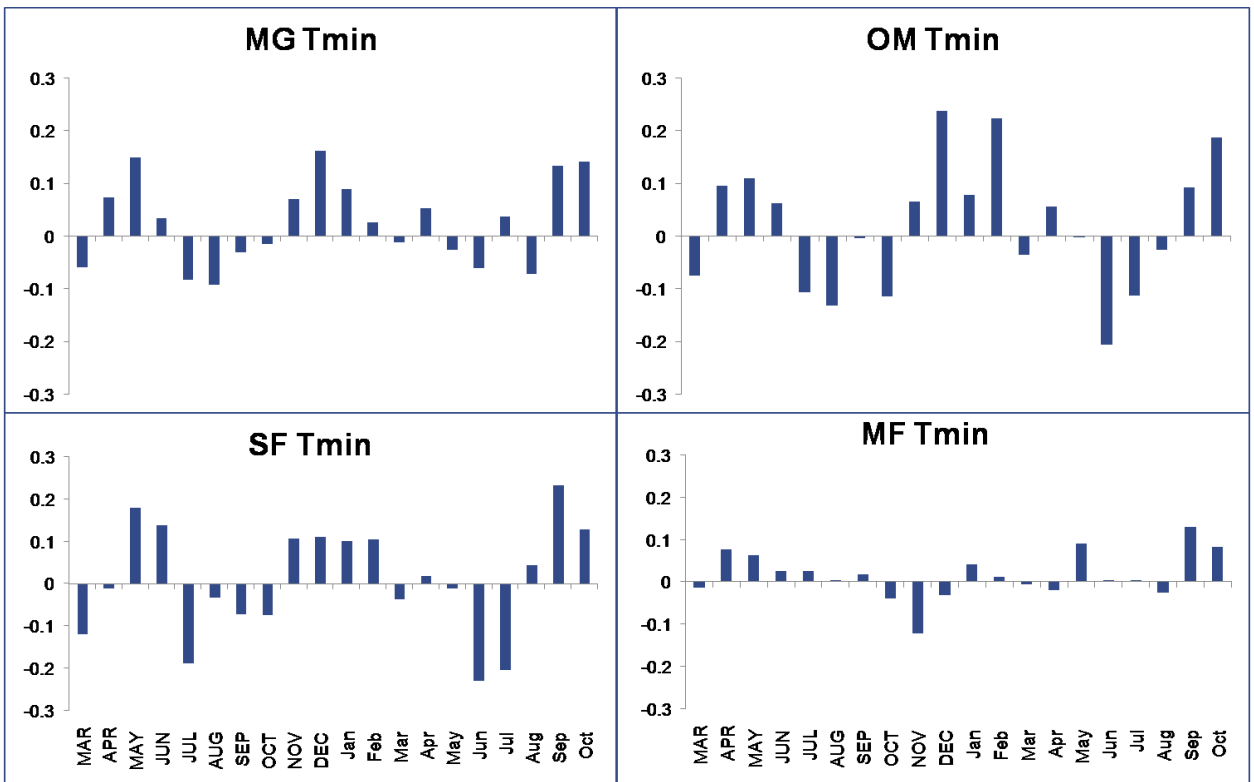


**Figure 14.** Correlations between minimum temperature and the residual chronology of *Picearubens* at four forests in Western Massachusetts.
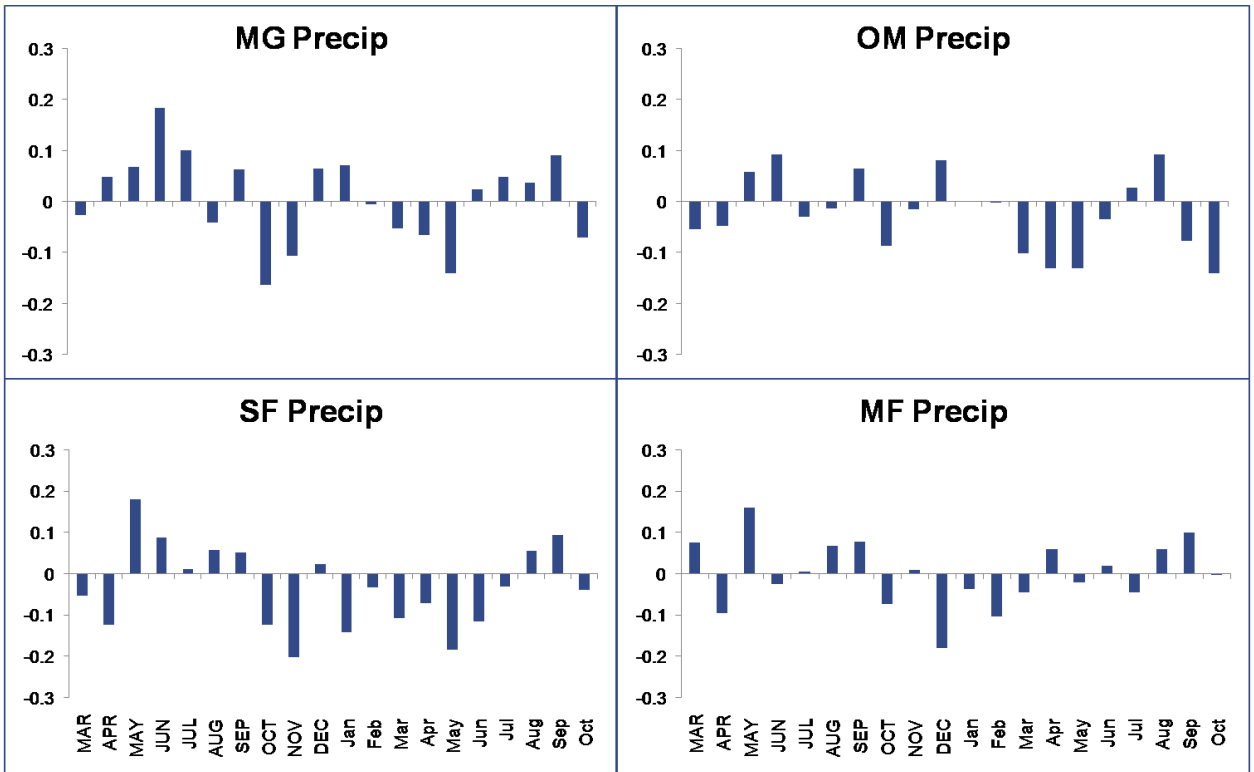
**Figure 15.** Correlations between precipitation and the residual chronology of *Picearubens* at four forests in Western Massachusetts.
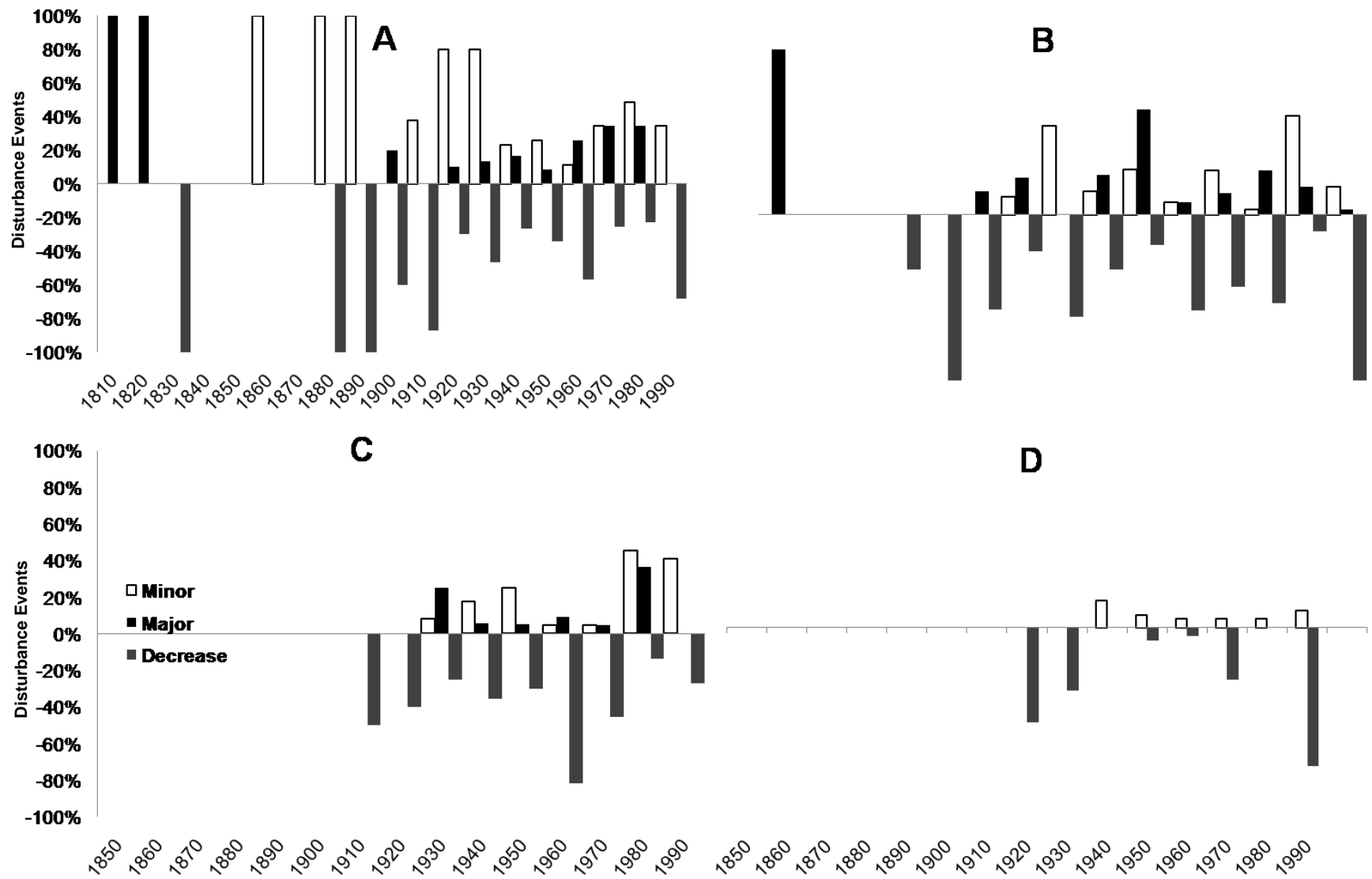
**Figure 16. Graphs of minor (50% growth increase) and major (100% growth increase) growth release events; and declines (50% growth decrease) at each site, tallied by decade and standardized based on sample depth at each decade.**
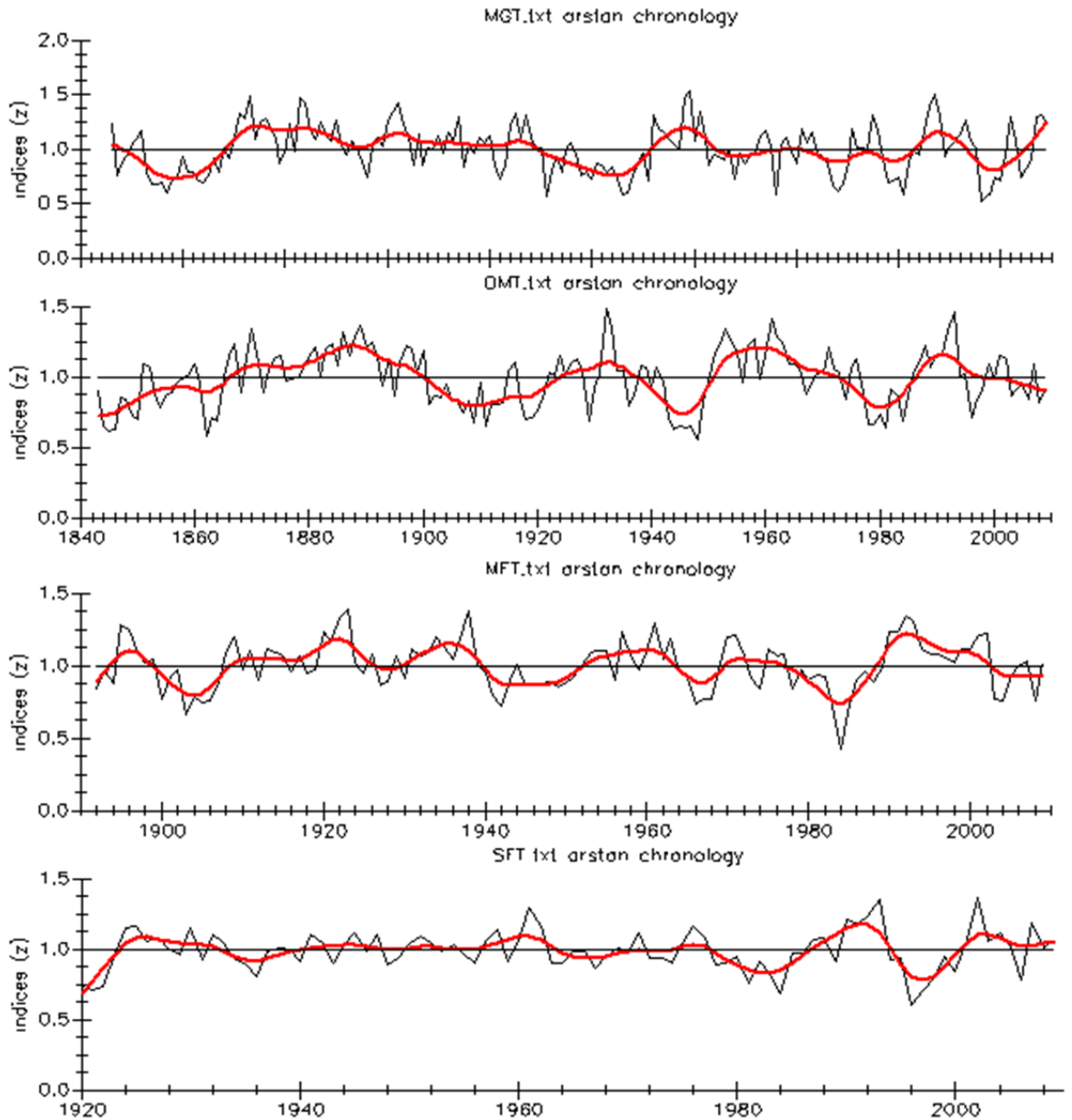
**Figure 17.** ARSTAN ARSTAN chronology, showing similar trends to residual chronology, but with auto-correlation pooled and added back to the residual chronology, with a smoothing spline applied.

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