Using dendroecological techniques to interpret the response of trees to environmental change at Vermont Monitoring Cooperative's Mount Mansfield study site

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Abstract

A number of tree species in Vermont have undergone documented decline in the 20th century, most notably red spruce and sugar maple. However, there is also varied and conflicting evidence about how these trees are responding to more recent changes in climate and atmospheric deposition. Here, we examine the growth, relative growth rates, and vigor of five key tree species in the Northern Forest growing in Mt. Mansfield State Forest: sugar maple (*Acer saccharum* Marsh.), red spruce (*Picea rubens* Sarg.), red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis,* Britton), and balsam fir (*Abies balsamea,* [L.] Mill.). We found baseline differences in past as well as present growth; with red maple and yellow birch having the highest mean basal area increment (BAI) growth, and sugar maple and balsam fir, the lowest. When growth was converted into a Z-score that compares recent growth (2008-2012) to mean growth since 1980 for each species, red maple and red spruce had growth above, yellow birch and balsam fir had growth that was indistinguishable, and sugar maple had growth that was below their respective means. Although many year-to-year declines in growth were likely associated with specific (often localized) stress events, protracted patterns in growth (e.g., the recent increases in red spruce and red maple growth) were more likely associated with broader climate or deposition trends. Based on our assessments with other chronologies, growth at Mt. Mansfield for these species aligns with regional trends and may indicate that patterns assessed here are indicative of the broader region.

Preamble

We are at a time of great potential change and stress for forest trees in Vermont and the broader Northern Forest. Existing forests reflect temporally and spatially complex land use change in the 19th and 20th centuries that has included extensive deforestation, agricultural expansion, and subsequent reforestation. Resulting second growth forests were then subjected to novel anthropogenic stresses in the 20th century, notably acid deposition-induced nutrient perturbations that altered forest health and productivity and has resulted in the observed decline in some tree species. In addition, anthropogenic carbon dioxide (CO_2) emissions have provoked climate change that may shift the competitive balance among forest species, further taxing and changing forest ecosystems. These and other threats to forest structure and function (e.g., a litany of invasive pests and pathogens) combine to create great uncertainty about the trajectory of the forest systems that comprise the majority of our landscape and support fundamental ecosystem services upon which all

life depends. The first step in assessing this trajectory of change is to establish a baseline for comparison. This report outlines one step in the establishment of this baseline. We describe the comparative assessment of the growth and vigor of five key tree species within the Vermont Monitoring Cooperative's long-term study site located in Mt. Mansfield State Forest, Vermont.

Introduction

While some tree species in Vermont have experienced growth declines, decreased vigor, and increased mortality in recent decades, others appear to be healthy and stable. Symptoms of both red spruce (*Picea rubens* Sarg.) and sugar maple (*Acer saccharum* Marsh.) decline have been observed since the mid-twentieth century (Westing 1966, Johnson et al. 1986). For both sugar maple (Schaberg et al. 2006, Huggett et al. 2007) and red spruce (DeHayes et al. 1999), well-documented health and productivity declines are associated with anthropogenic acidic deposition and associated calcium depletion. However, other species, such as red maple (*Acer rubrum* L.) (Abrams 1998), yellow birch (*Betula alleghaniensis,* Britton) (van Doorn et al. 2011), and balsam fir (*Abies balsamea,* [L.] Mill.) (Hornbeck et al. 1987), are notable as being stable or only exhibiting periods of limited decline.

Added to the stress of anthropogenic pollutants and decades of soil cation depletion, the region is also experiencing changes in climate, with Vermont listed as one of the states in the US undergoing the largest change in annual temperature (IPCC 2014). According to the IPCC (2014), global warming of approximately 2°C above the pre-industrial baseline will very likely lead to more frequent heat and precipitation extremes over most areas of North America, though most precipitation will fall as rain rather than snow. In the Northeast, climate models predict an increase of 2.2°C by 2050 under continued high greenhouse gas

emissions scenarios and about 1.7°C under low emission conditions (Northeast Climate

Impacts Assessment Synthesis Team 2007). In addition, many climate models also indicate

larger inter-annual variation in both temperature and precipitation (Hayhoe et al. 2007)

and higher variability in resulting weather patterns may become the norm.

Although precipitation is not as easy to predict as temperature, by the end of the

century, seasonal precipitation in the Northeast is projected to increase approximately 15%

in winter, 10% in spring, and 5% in fall, but exhibit no change in summer (high emission

scenario) (Betts 2011). An earlier timing of spring snowmelt and increased runoff from

heavier rainfall events, possibly coupled with increased evaporation with co-occurring

elevated temperatures, could increase the frequency of summer droughts (Northeast

Climate Impacts Assessment Synthesis Team 2007).

The combination of increased temperature and precipitation in winter is expected

delay the onset and decrease the depth and duration of snowpack (Groffman et al. 2012).

Because snow insulates the soil from severe freezing and minimizes the frequency and

extent of freeze/thaw cycles, reduced snowpack could lead to greater soil freezing that can

damage roots and disrupt nutrient cycles and plant carbon relations (Comerford et al.

2013).

Projected changes in climate are consistent with the observed trends evident in the

region. Since 1960, the annual mean temperature has increased by 1.1°C, with winter

temperatures rising 2.5°C (Hayhoe et al. 2007). In Vermont from 1960-2008, summer and

winter temperatures have increased 0.22 (±0.07)°C and 0.5 (±0.16)°C per decade,

respectively (Betts 2011). This warming has resulted in a lengthened growing season

(increase of 3.7 (±1.1) days per decade), more winter precipitation falling as rain rather

than snow, reduced snowpack in some winters, earlier spring snowmelt (freeze period has

decreased 3.9 (±1.1) days per decade), and more frequent days with temperatures above

32.2°C (Northeast Climate Impacts Assessment Synthesis Team 2007, Betts 2011).

Precipitation has increased by 15-20% in Vermont since the 1960s, with a 67% increase in

the amount falling during very heavy precipitation events (Northeast Climate Impacts

Assessment Synthesis Team 2007). Continued changes in temperature, precipitation, and

depth, duration, and extent of snowpack could push trees beyond historic environmental

thresholds to which they are adapted and result in reduced competitive capacity, growth,

and survival. In addition, these changes are also coupled with increased atmospheric CO_2

concentration and changes in other anthropogenic atmospheric inputs (e.g. sulfate,

ammonium, etc.).

   Although evidence of anthropogenic stresses continues to mount within forests,

there is limited evidence of clear trends in forest response. Indeed, one would expect that

some species might benefit from climatic and other changes while others would not. Among

other factors, atmospheric CO_2 concentrations have been shown to provide a fertilization

effect in some plants (Soule and Knapp 2006, Martinez-Vilalta et al. 2008), and when

combined with increases in temperatures, growing season length, and precipitation, could

all promote increased growth for some species or elevations (Salzer et al. 2009) over

others. Whereas the declines of several tree species associated with acid deposition are well

documented in the region, the literature has also noted that some of these chronically

stressed trees are experiencing recent growth increases (Kosiba et al. 2013) and possible

range extensions (Beckage et al. 2008), hypothesized to be associated with changes in

climate. However, relatively few studies have sought to examine the relative growth trends

for the dominant tree species in Vermont and compare past to present growth in light of

these regional changes in climate.

   With both reported negative and positive changes in growth attributable to

changing abiotic factors for various tree species in New England, an important question to

ask is, what are the net influences of changes in abiotic factors on the productivity of tree species? The best method of assessing species response to stress is to establish baseline data for contemporary comparisons and as a future reference. Long duration and annually resolved tree growth increment cores provide a method to examine both past and current growth, as well as examine possible trajectories for future growth. How will Vermont's tree species respond to changes in local temperature, atmospheric CO_2, growing season length, anthropogenic atmospheric inputs and other perturbations?

The overall goal of this project was to assess recent patterns and trends in forest growth on the Vermont Monitoring Cooperative's (VMC) long-term study site located in Mt. Mansfield State Forest (44.5439° N, 72.8143° W), Vermont, using xylem growth (radial annual increment) measurements for five key forest tree species: sugar maple, red spruce, red maple, yellow birch, and balsam fir. Species were chosen because they were the dominant components of the boreal (red spruce and balsam fir) or northern hardwood (sugar maple and yellow birch) forests, or because the species has experienced increased dominance in this latter forest type (red maple; Abrams 1998). A dominant component of the northern hardwood forest, American beech (*Fagus grandifolia* Ehrh.), was not assessed because its growth dynamics have been altered following widespread damage from the beech bark disease complex (Gavin and Peart 1993). Target species were sampled along an elevational gradient to capture trends in the three major forest cover types – deciduous, mixed, and coniferous forests – replicated in three watersheds.

We hypothesized that trees will have different growth rates dependent on species, elevation, and year. We also expected that some species will have reduced growth rates in recent years, most notably sugar maple, which has experienced geographically broad decline since the 1980s (Horsley et al. 2002), but potentially yellow birch too, which has had more limited recent decline elsewhere in New England (van Doorn et al. 2011).

Conversely, we expected that red spruce will have increased growth rates at Mt. Mansfield synchronous to a broader regional upsurge in growth, which is of unknown origin (Kosiba et al., 2013). Though this current study was of limited spatial extent, by comparing the annual growth of these species at different elevations and aspects, and assessing local trends to patterns elsewhere we hoped to gain a better understanding on relative growth rates among key forest species. By associating the nature and timing of growth trends relative to local weather, pollution, and forest health data, we also sought to assess how climate may have influenced species relative growth rates and productivity.

Methods

Plot Selection

Elevational transects were set up in three of the four watersheds on Mt. Mansfield: Brown's River, Stevensville Brook, and Ranch Brook. No transect was established in the fourth watershed because this area has experienced anthropogenic disturbance associated with a commercial ski area. Along each of these transects, three plots were selected – one within each of the following elevational zones: low (< 760 m asl), mid (760-880 m) and high (> 880 m) (*N* plots = 9, Figures 1 and 2). Precise elevation and location of plots was dependent on the number of dominant or co-dominant trees present per species (see Appendix I for plot information).

At each plot, 10-12 trees of each of the target tree species were selected with approximately equal distribution around plot center. Trees with obvious bole or crown damage or those growing in anomalous conditions were not selected for study. At low elevations, we sampled red maple, sugar maple, and red spruce; at mid elevations we sampled, sugar maple, yellow birch, and red spruce; and at high elevations we sampled red spruce and balsam fir (Figure 2). All species names and codes follow Natural Resource

Conservation Service (NRCS) PLANTS database specifications (NRCS 2014). Due to differential species densities across the landscape, plots were of variable radius. All trees were tagged with blue aluminum tree tags at breast height. Tags either faced plot center or if near a hiking trail were oriented away from the trail.

Figure 1: Map of nine dendrochronological plot locations in the Mt. Mansfield State Forest, Vermont, showing three watershed transects (black lines), each with three plots (red dots) located within low, mid, and high elevational zones.
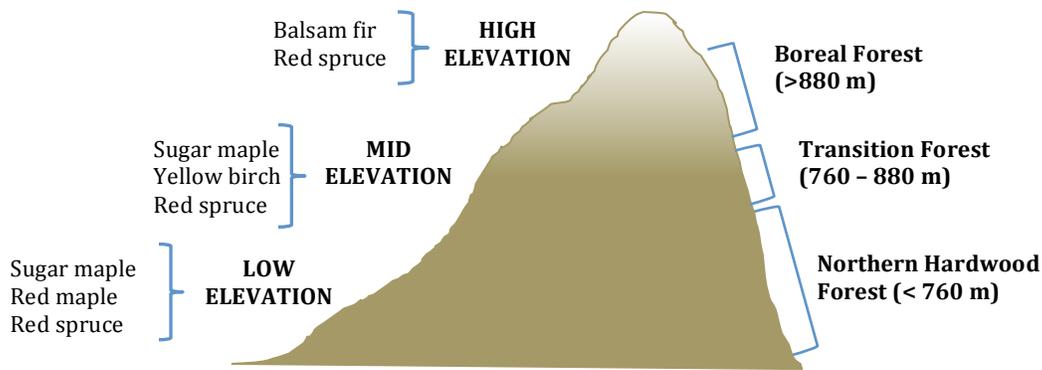
Figure 2: Diagram of the sampling scheme on Mt. Mansfield. This scheme was replicated in three watersheds (Brown's River, Stevensville Brook, and Ranch Brook).

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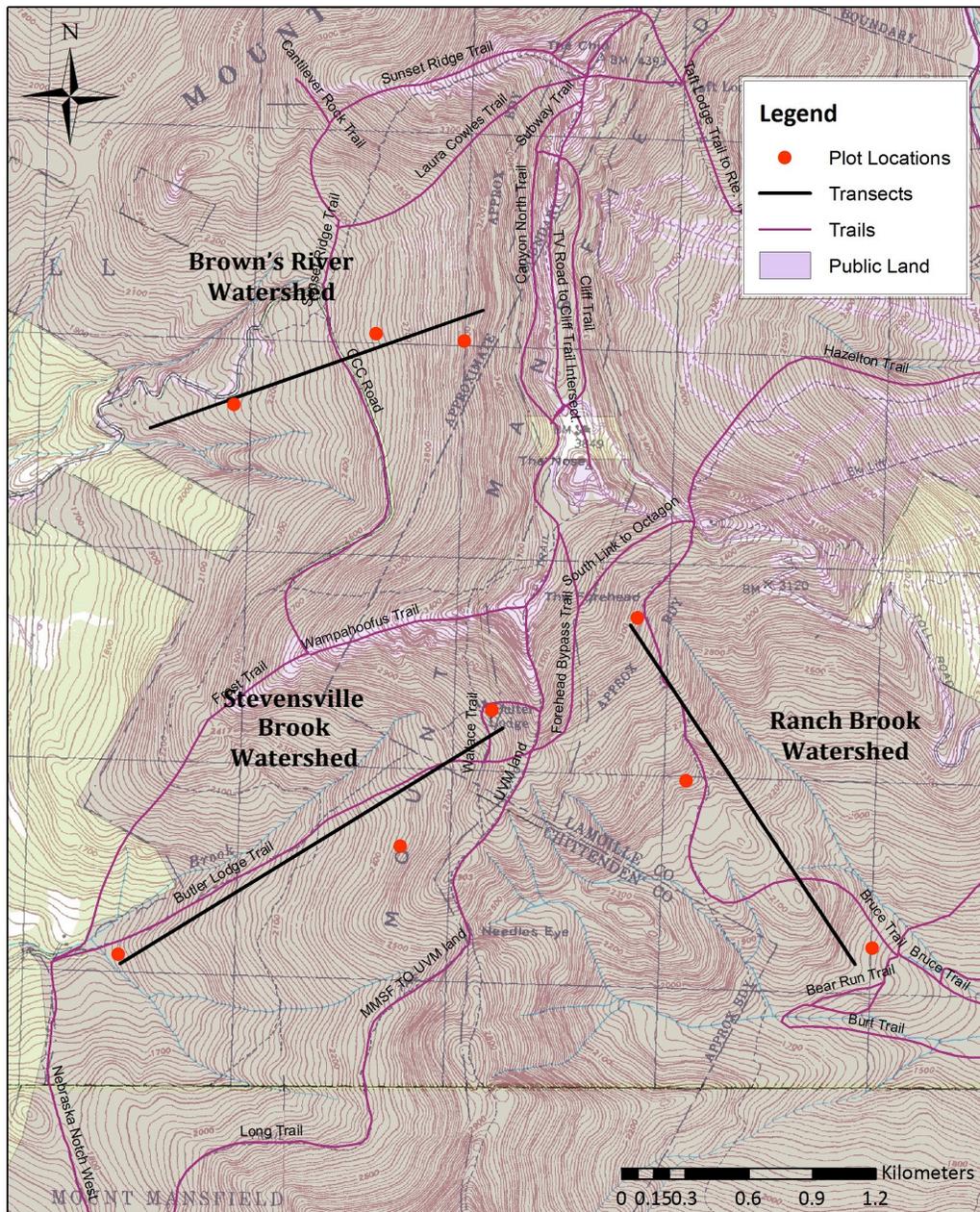
Dendrochronology

Selected trees were increment cored following standard dendrochronological techniques (Stokes and Smiley 1968) in the fall of 2012. Two xylem increment cores (5 mm) were collected per tree at stem DBH (diameter at breast height, 1.37 m above ground level) at 180° to each other and perpendicular to the dominant slope. Crown position (dominant or co-dominant) and DBH were also recorded. For red spruce and balsam fir, sapwood was immediately marked on the tree core with a permanent marker. Linear sapwood

measurements were averaged by tree and converted into area using tree DBH. Sapwood area has been shown to be a good indicator of foliar biomass for conifers (Grier and Waring 1974, Kendall Snell and Brown 1978).

Following collection, cores were air dried, mounted in grooved wooden blocks with water-soluble glue, and sanded with progressively finer grit sandpaper (ranging from 100-1500 grit depending on species). Cores were visually crossdated using the list method (Yamaguchi 1991) and microscopically measured to 0.001 mm resolution using a Velmex sliding stage unit (Velmex Inc., Bloomfield, NY) with MeasureJ2X software (VoorTech Consulting, Holderness, NH). The computer program COFECHA was used to detect and correct for potential crossdating errors in ring series (Holmes 1983). Combined with visual crossdating, COFECHA statistically assesses the annual alignment of rings between cores and provides a quality control for accurate annual resolution of tree-ring data (Spear 2010). Individual cores were discarded if they were poorly correlated with the master chronology (i.e., below Pearson critical correlation level of 0.328 [99% confidence level]). These cores had low year-to-year variability in growth or unusual growth trends compared to the sampled population. Tree age was calculated using the maximum number of rings per tree if pith was evident or estimated per core using the using a pith indicator (Speer 2010) if pith had not been reached. Therefore, tree age was estimated based on rings at breast height.

Raw ring widths were averaged by tree (N trees = 265) and converted into basal area increment (BAI, cm^2 year^{-1}) assuming a circular outline of stem cross sections (Cook and Kairiukstis 1990) following the formula:

$$BAI = \pi(R_n^2 - R_{n-1}^2)$$

Where R is the tree's radius, derived through measured diameter at breast height and bark thickness, and n is the year of tree ring formation. BAI is considered a more meaningful indicator of tree growth from a physiological standpoint as BAI standardizes annual

increments relative to basal area, thus providing an indication of annual stemwood

production while accounting for the effects of stem geometry on radial growth associated

with tree-maturation (West 1980, Hornbeck and Smith 1985, LeBlanc 1992).

Dendrochronological statistics per species per plot – series intercorrelation,

autocorrelation, and average mean sensitivity – were calculated by COFECHA. Series

intercorrelation is a measure of the stand-level signal, while mean sensitivity is a measure

of the year-to-year variability in the ring widths (Speer 2010). According to Speer (2010),

these two statistics are the most comparable measures of a site-level signal and sensitivity

between sites. Autocorrelation is a measure of the correlation between successive rings in

the chronology (Speer 2010). In the Northeast autocorrelation among ring widths is

common since weather patterns, defoliation events, and stand dynamics, for example, in

preceding years can have a substantial impact on current-year ring formation.

Series intercorrelation and sample depth were used to calculate the expressed

population signal (EPS) for each species per plot using the equation presented by Wigley et

al. (1984).(see Appendix 1 for equation). Chronologies were truncated at the year when the

EPS value fell below 0.85, which is the accepted cutoff when the plot-level signal is eclipsed

by the individual tree signal and thus is a less reliable indicator of stand-wide trends (Speer

2010). Based on EPS values (see Appendix I) for all analyses, aside from looking at general

trends, only the common time period (1980-2012) was used for cross-species comparisons.

This timeframe also aligns with the period of most interest by VMC.

Due to violations of homogeneity of variance, for statistically robust comparisons

among species, elevational bands, and transects, mean BAI per species per plot was

converted to a standard score (Z-score) with the following formula:

$$Z = \frac{y_i - \chi}{\sigma}$$

Where y_i is the mean BAI in year i, and χ and σ are the grand mean and standard deviation for the common period (1980-2012). An additional benefit of this standardization technique is that it allows easy visualization of positive and negative growth trends relative to the species' average growth at that site. It also facilitated comparisons between species that have disparate growth rates. In order to broadly assess tree productivity and response over time, some results are presented in BAI while others as Z-scores.

Crown vigor and dieback assessments

For all sampled trees, crown vigor and branch dieback were visually assessed between 23 August and 5 September 2013 using binoculars by two researchers to minimize observer bias. We followed established methods utilized by both Forest Inventory and Analysis (FIA) and the North American Maple Project (NAMP) programs. Crown vigor was rated on a 1-5 scale: (1) highly vigorous crowns without major branch dieback and less than 10% branch or twig mortality, (2) light decline with branch and twig mortality present and between 10-25%, (3) moderate decline with branch and twig mortality between 25-50%, (4) severe decline with extensive branch mortality and greater than 50% branch and twig dieback, or (5) dead (no trees selected for increment coring were dead; complete ratings listed in Appendix II) (Cooke et al. 1996, USDA Forest Service 2006). We then estimated the proportion of the crown silhouette with branch dieback, defined as branch mortality that begins at the terminal portion of a limb and progresses downward, following a 5-point scale from 0-100% (scale listed in Appendix II) (Cooke et al. 1996, USDA Forest Service 2006).

Tree density and competition sub-plots

In each of the 9 plots, two trees per target species were selected to mark the center of a 7.23 m (24 ft) radius sub-plot following FIA guidelines (USDA Forest Service 2006) to

allow for ease of comparison to other datasets and future data collection. Under this configuration, low and mid-elevation plots had six sub-plots each, while high plots had four. Selected trees were chosen to represent the spatial extent of the plot. Within the sub-plot, all woody stems >12.7 cm (>5.0 in) DBH were recorded for species, DBH, crown class, and vigor rating (described previously). Density plots were conducted concurrent with crown vigor and dieback assessments. Sub-plot data were summed and then averaged per plot. These data were converted to mean basal area (BA, m^2) per hectare and analyzed for differences using ANOVA followed by Tukey-Kramer HSD tests.

Climate and deposition data

Climate data (maximum and minimum monthly temperature and total monthly precipitation) for 1980-2012 were obtained from the PRISM Climate Group (PRISM Climate Group 2004) using the latitude and longitude of each plot center. These widely used datasets were created using the PRISM (Parameter-elevation Regressions on Independent Slopes Model) climate mapping system using point measurements of precipitation, temperature, and other climatic factors to produce continuous estimates of monthly, yearly, and event-based climatic parameters (PRISM Climate Group 2004). From these data, mean monthly temperature, seasonal mean temperature (Winter: previous December – February, Spring: March – May, Summer: June – August, Fall: September – November), annual mean temperature, seasonal precipitation totals were calculated. Data were also lagged one year to assess the effect of previous year's temperature and precipitation on current year's growth. Deposition data was obtained from the National Atmospheric Deposition Program (NADP) for Mt. Mansfield (Underhill 44.5283° N, 72.8684° W, 399 m asl)(National Atmospheric Deposition Program 2014). We also used annual atmospheric CO_2 concentration (NOAA Earth System Research Laboratory Global Monitoring Division 2013),

Vermont Palmer Drought Severity Index (PDSI) (National Drought Mitigation Center 2014), and growing degree days (GDD; for Burlington International Airport) (NOAA National Weather Serivce 2014).

Analyses of growth trends

Standardized mean BAI for each plot per species was tested through ANOVA analyses using a model with year and species and the interaction of year x species as sources of variation. Since red spruce was the only target species to grow at all elevational bands, a second model was constructed for red spruce using elevation, year, and the interaction of year x elevation. Following this, climate parameters were added to the model since the influence of "year" is likely related to changes in yearly weather patterns (e.g., droughts, heat waves, spring frosts) that alter photosynthesis, respiration, and growth. Deposition data was also included in these models to assess how changes in these inputs alter growth. To limit parameters included in the models, we used principal component analysis (PCA) to examine the most influential drivers to each species' growth. Final model selection was done using forward stepwise linear regressions with AIC (Akaike information criterion). All statistical analyses were conducted using JMP Version 10 software (SAS Institute Inc., Cary, NC) and considered significant if $P < 0.05$.

Comparisons with other chronologies and datasets

Other tree ring chronologies collected by the authors or affiliates were used to compare growth trends to other locations in the region. All chronologies were collected following similar methods described above and converted into BAI. Due to age limits of some chronologies, we constrained analyses to 1950-2012. Spatial data of all aerial defoliation surveys in Vermont from 1985 to 2012 (Vermont Agency of Natural Resources

Department of Forest Parks & Recreation 2013) were also used to examine possible events that may account for years of low growth in tree ring chronologies.

Results and Discussion

Chronology statistics

In total, 265 trees were used for this study. Summary statistics and data on the nine plots and resulting chronologies can be found summarized by species and elevational zone in Table 1 or by species per plot in Appendix I. Chronology statistics presented here were comparable to those from other dendrochronological studies, previous work by our group, and tree-ring summary statistics provided by the National Climatic Data Center (NOAA National Climatic Data Center 2008) for these species. We observed the highest mean sensitivity in sugar maple chronologies (mean sensitivity for all sugar maple: 0.314), shown by the large year-to-year variation in ring width, though mean sensitivity was higher at the mid elevation plots than the low (0.325 and 0.304, respectively). This suggests that these trees were more sensitive to changes in environmental conditions while balsam fir (0.209) and red maple (0.225) exhibited comparably low mean sensitivity. On Mt. Mansfield, these two species had more complacent growth trends with low year-to-year variations in growth. Interseries correlation, a measure of how similarly responsive trees of a species are within a plot, was highest for balsam fir (0.583) and red spruce (0.552), indicating that these species have a much more cohesive stand-level response than the three deciduous species, which may be more affected by stand dynamics and/or microsite conditions.

Table 1: Tree ring data listed by species per elevational zone across the three watersheds. Elevational zones are: low < 760, mid 760-880, and high > 880 m asl. Mean diameter was at breast height (DBH 1.37 m) (± SE). Mean age was based on the mean number of rings at breast height. Interseries correlation and mean sensitivity from COFECHA output were averaged by species and used to calculate expressed population signal (EPS) per species. Maximum mean basal area increment (BAI cm^2) ± SE and year of this growth (indicated in parentheses) are also presented. Years of max BAI lists the five largest BAI values by the year in which they occurred, from smallest to largest.

Sp.	Elev. Zone	N trees	Mean DBH ± SE	Mean age ± SE)	Mean BAI ± SE	Inter. corr.	Mean Sen.	Mean EPS	Max. mean BAI ± SE	Yrs of max BAI
Red maple	Low	28	39.6 ± 0.3	90.0 ± 0.9	14.6 ± 0.2	0.514	0.225	0.90	29.8 ± 5.8 (2012)	2006, 2008, 1995, 1988, 2012
Sugar maple	Low	29	32.5 ± 0.2	95.9 ± 0.7	8.8 ± 0.1	0.474	0.304	0.90	14.2 ± 1.1 (1994)	1984, 1991, 1995, 1985, 1994
	Mid	34	28.2 ± 0.2	93.1 ± 0.7	6.9 ± 0.1	0.466	0.325	0.91	10.5 ± 2.3 (1983)	1966, 1967, 1975, 1984, 1983
Yellow birch	Mid	34	43.2 ± 0.3	101.1 ± 0.8	15.1 ± 0.2	0.467	0.286	0.91	27.2 ± 0.6 (1973)	1982, 1969, 1974, 1970, 1973
Red spruce	Low	31	34 ± 0.3	142.7 ± 1.8	8.2 ± 0.1	0.519	0.257	0.92	18.1 ± 3.4 (2012)	2002, 2010, 2011, 1993, 2012
	Mid	34	41.5 ± 0.3	165.5 ± 1.5	11.7 ± 0.2	0.559	0.254	0.93	27.9 ± 4.0 (2012)	1993, 2009, 2011, 2010, 2012
	High	41	23.5 ± 0.2	86.7 ± 0.8	5.3 ± 0.1	0.579	0.236	0.95	13.2 ± 3.4 (2012)	2007, 2011, 2009, 2010, 2012
Balsam fir	High	34	23.4 ± 0.1	77.9 ± 0.6	5.4 ± 0.1	0.583	0.209	0.94	10 ± 2.2 (2001)	1990, 1987, 1993, 1995, 2001

Tree ages

Overall, there was a wide range of tree ages observed at the nine plots (Table 1), with significant differences among the species. Tree ages were not significantly different among the watersheds or elevational zones. However, within the elevational zones there were some differences among species. At high elevations, red spruce was found to be significantly older than balsam fir ($P < 0.04$). At mid elevation, red spruce was also significantly older than the other two species, yellow birch and sugar maple ($P < 0.003$). At

low elevations, however, the three target species were not significantly different in age ($P <$ 0.9). Despite some differences in tree age, there was no significant relationship between recent growth (examined as mean BAI 2008-2012) and tree age ($P < 0.2$).

Site-based land use as predisposing factor

Land use history has left a legacy of complex stand dynamics in the forests on Mt. Mansfield, which is evident in the ages of trees of certain species at the three elevations. In the absence of a significant natural disturbance, it is more likely that selective logging has resulted in a difference in ages among the species of dominant and co-dominant trees. Indeed, Cogbill (1996) outlined multiple logging events in the Stevensville Brook Watershed, and it is well-known that widespread harvesting occurred in the other watersheds on Mt. Mansfield as well. In his report, Cogbill (1996) noted that the species of most interest due to its lightweight and easy to cut wood, particularly at the end of the 1800s, was red spruce. Despite this, the mid elevation plot in the Stevensville Brook Watershed was located within a band of large, emergent, and quite old red spruce trees. Similarly old red spruce trees were found in the Ranch Brook watershed. Other research speculates that these trees were either excluded from logging due to their small size at the time (Hannah 1999), though perhaps there was also a higher density of red spruce prior to land clearing (Cogbill et al. 2002). Regardless of the cause, the young ages of some stands do impose a hurdle when examining trends in growth over time.
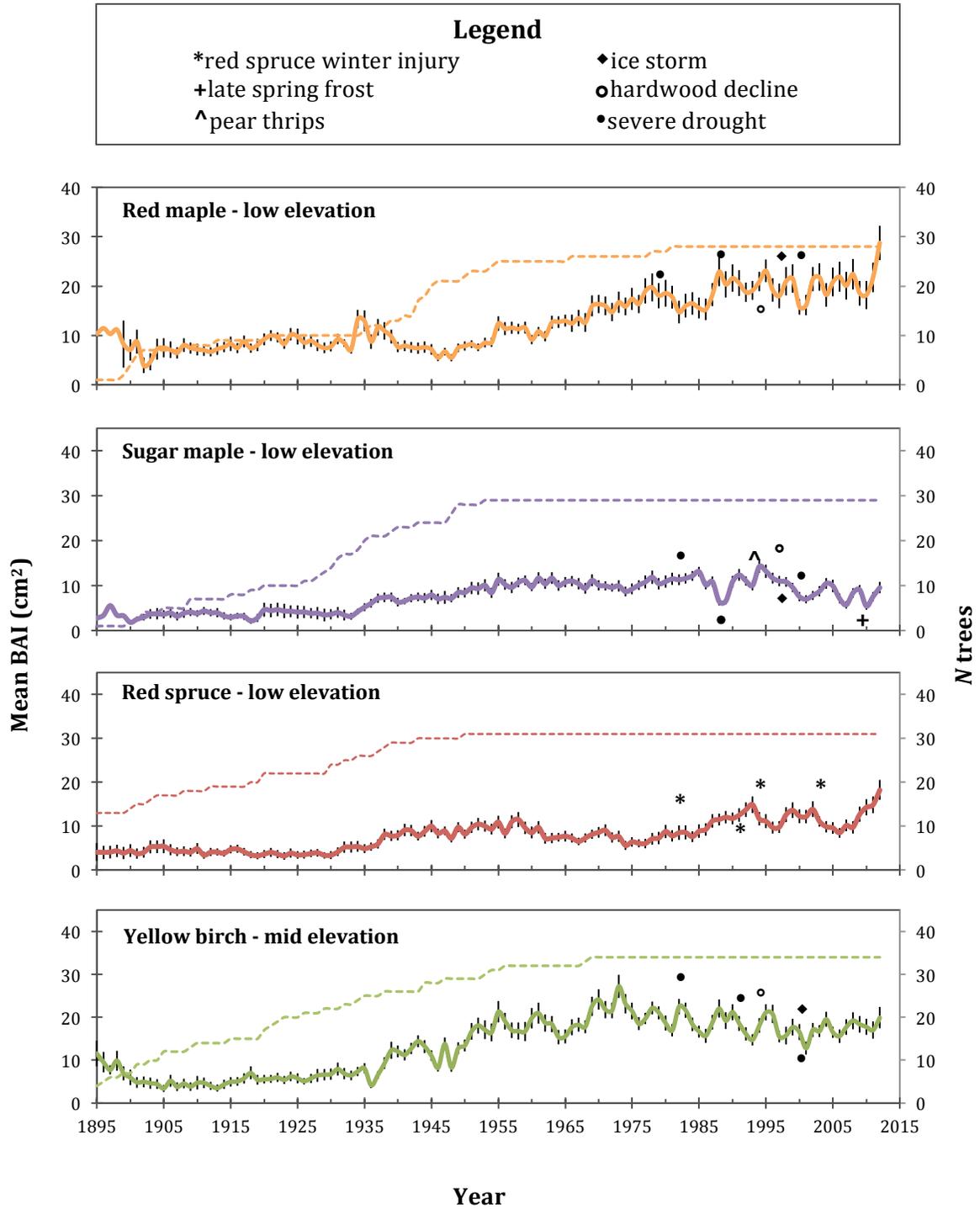
Mean BAI and years of highest growth

Yellow birch and red maple had the highest mean BAI (mean BAI ± SE: 15.1 ± 0.2 and 14.6 ± 0.2, respectively)(Table 1), while balsam fir and red spruce at high elevation had the lowest (5.4 ± 0.1 and 5.3 ± 0.1, respectively). For red spruce at all elevations and red

maple, highest growth was in 2012 and at least three of the five largest growth years occurred within the decade prior to sampling (Table 1). Indeed, for red spruce at high elevation, the five years of largest growth occurred within the last decade. In contrast, sugar maple had maximum growth that was not drastically higher than the mean and the five years of highest growth occurred in the 1980s and 1990s for low elevations and 1960s through the 1980s for mid elevations. Likewise, the years of greatest growth for yellow birch occurred in the 1960s through the 1990s.

Using a Wilcoxon non-parametric test (due to unequal variances), we found significant differences between the species (regardless of elevation) for BAI growth ($P < 0.0001$). Looking at pairwise comparisons (Wilcoxon Each Pair test), we found that all species were significantly different from the others (for all pairs $P < 0.03$), from largest to smallest BAI: red maple, yellow birch, red spruce, sugar maple, balsam fir. When we looked at BAI growth per species by elevation, all species were significantly different from the other target species at that elevation (both overall and pairwise, $P < 0.0001$). At high elevation, red spruce had significantly higher BAI than balsam fir. At mid elevation, yellow birch had significantly higher BAI than red spruce and sugar maple, with red spruce being significantly higher than sugar maple. At low elevation, red maple had significantly higher BAI than red spruce and sugar maple, with red spruce being significantly higher than sugar maple (Table 1).

Though we would expect BAI to decrease with increasing elevation (Coomes and Allen 2007), trees at mid elevations had significantly higher growth than those at both low and high elevations, and low elevation trees had significantly higher growth than those at high elevation ($P < 0.0001$ for overall test and all pairs). For the two species we examined at multiple elevations (red spruce and sugar maple), growth was lower at mid compared to

low elevation for sugar maple, but for red spruce, growth was highest at mid elevation (Table 1). However, there were no significant differences in growth among the transects.
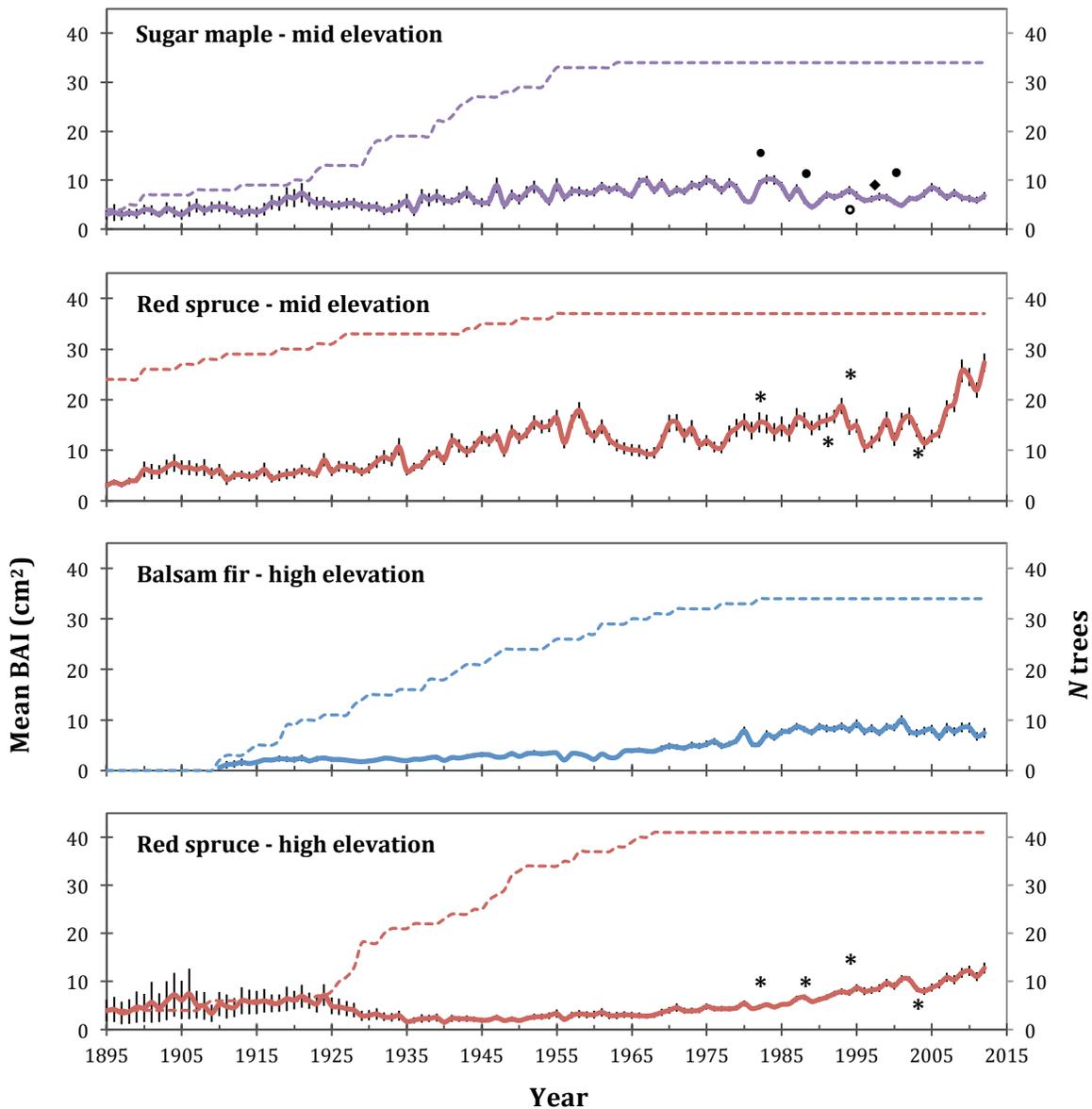

Legend
*red spruce winter injury   ◆ice storm
+late spring frost   ○hardwood decline
^pear thrips   •severe drought

Figure 3: Mean (± SE) basal area increment (BAI, cm², solid line) per species per elevational zone (low < 760, mid 760-880, and high > 880 m asl) from 1895-2012. Number of trees contributing the mean shown with dashed line. Symbols represent abiotic and biotic stresses that were reported for the region and may help explain growth declines in given years (Dupigny-Giroux 1999, Lazarus et al. 2004, Hufkens et al. 2012, Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2013).

Chronologies per species per elevation (1895-2012)

Sample depth

Mean BAI (± standard error [SE] of the mean) per species per elevational band from 1895-2012 are depicted in Figure 3, with the number of trees (N) contributing to the mean (sample depth) on the z-axes. Evaluation of sample depth illustrates differences among the species and elevations. At high elevation, red spruce and balsam fir had similar sample depths, with both species maintaining half of the trees contributing to the mean in the early 1930s. In 1895, red spruce retained less than 1% of the trees used for this study; balsam fir had none. In 1895 at mid elevation, however, red spruce preserved ~65% of the trees contributing to the mean, while for yellow birch and sugar maple it was only 12%. In contrast, in 1895 at low elevation, red spruce retained 4% of trees, while for red maple and sugar maple it was less than 1%.

Possible causes of changes in growth

Figure 3 also depicts possible causes for some of the changes in growth due to biotic and abiotic factors based on available data. Some of the factors that may have contributed to low growth in a given year are speculative, based on synchronous declines across plots for a species and known defoliation or stress events in the region for that time period (i.e., based on published research in the region or annual reports and over-flight images produced by Vermont Agency of Natural Resources Department of Forest Parks & Recreation). Comparisons of the chronologies depicted in Figure 3 highlight that the five species often experienced changes in growth that were either species- or elevation-specific. As a preliminary assessment of possible causes of the more obvious deviations in growth, we compared the timing of these changes to historic forest health data. For example, sugar maple at low elevation had low growth in 2010 possibly due to the late spring frost that occurred that year in May (**+** in Figure 3) (Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2010, Hufkens et al. 2012), while this decrease in

growth was not as dramatic for sugar maple at mid elevation. This aligns with the elevational patterns associated with the spring frost in 2010: the most severe frost damage occurred at 573 ± 157 m asl (Hufkens et al. 2012), which is below our mid elevational zone (760-880 m). While yellow birch may have been affected by this frost (Hufkens et al. 2012), deceases in growth were not as uniform across plots as we see in sugar maple at low elevation, most likely as these trees were above the band of highest frost damage and because leaf expansion in yellow birch occurs after sugar maple (Hufkens et al. 2012).

A severe drought reported for Vermont from 1988-89 (Dupigny-Giroux 1999) may have impacted sugar maple at all plots in both low and mid elevations as indicated by a large synchronous decrease in growth at this time (drought denoted with • in Figure 3) and was reported for other sugar maple (Kolb and McCormick 1993). Drought was also reported from 1980-81 (Dupigny-Giroux 1999), but growth declines were only evident for mid elevation sugar maple and yellow birch and were not as severe for trees growing at low elevation. A pear thrips (*Taeniothrips inconsequens* [Uzel]) infestation was reported for the eastern side of Mt. Mansfield in 1993 (Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2013), and may have affected sugar maple growth at low elevation. In addition, hardwood decline was recorded in over flight data for 1995 (Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2013)(o in Figure 3) and could have been responsible for the steep growth declines seen for both red maple and yellow birch at that time.

A severe ice storm (◆ in Figure 3) in 1998 that broke limbs and crowns of many hardwood species (Rhoads et al. 2002), was reported for mid and high elevation plots (Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2013). Wilmont (1998) noted the spatial pattern of the ice storm: western slopes of Mt. Mansfield had two bands of damage ~700-915 m asl (2700-3000 ft) and a second at the ridgeline,

while on the east side, ice was noted at all elevations, with severe damage at both ~670-915 m asl (2200 – 3000 ft) and on the summit. These areas of high ice loading align with our mid elevation zone (760-880 m asl), and may have impacted the high elevation plots, too. In addition, drought damage was reported for hardwood species at low and mid elevations in 1999 (Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2013) and likely caused the growth declines for red maple, yellow birch, and sugar maple evident in 1999 through 2000. Perhaps the combined effect of the ice storm followed by severe drought resulted in low growth in subsequent years.

For red spruce trees, all three elevational zones showed evidence of reduced growth attributable to the well-documented region-wide winter injury event in 2003 (Lazarus et al. 2004)(* in Figure 3). Although overflight surveys (Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2013) failed to document foliar damage to these plots in 2003 , the three plots of red spruce in the Stevensville Brook watershed used for this study were visually assessed for winter injury damage in 2003; damage to current-year's foliage for the low elevation plot was 13%, while it was much higher for the mid and high elevation plots at 75% and 70%, respectively (Lazarus et al. 2006, Schaberg et al. 2011). Previous studies by the authors have shown reduced growth for regional red spruce for up to four years following this event (Kosiba et al. 2013), and this decrease is also evident in the red spruce chronologies presented here. Winter injury in the region was also noticed in earlier years (Johnson et al. 1992, Lazarus et al. 2004), but the severity and extent of damage to red spruce growing on Mt. Mansfield is unknown.

Species growth comparisons

For some species, such as sugar maple at low elevation, the repeated stress of abiotic and biotic factors in succession may help explain prolonged growth declines. Sugar

maple at both low and mid elevations appears to have somewhat reduced growth. Although growth measurements reported here for sugar maple are low compared to the other target species, they are not atypical when compared to other dendrochronological studies in eastern North America (Duchesne et al. 2003, Long et al. 2009, Hansen in prep). Indeed, many of the years of low growth for sugar maple are likely attributable to specific biotic or abiotic events that have been reported in the literature (e.g., Duchesne et al. 2003, Kolb and McCormick 1993).

Yellow birch has a high degree of year-to-year and between-plot variation (e.g., large standard error bars); however, mean growth has remained relatively constant for multiple decades. Balsam fir at high elevation exhibit fairly consistent growth, with little year-to-year and between-plot variation. Even as sample size decreased back in time, the standard error of the mean for balsam fir remained small.

It is also apparent in Figure 3 that red spruce trees have experienced a recent growth increase, which is consistent with other data, but of unknown cause (Kosiba et al. 2013). While this recent uptick in growth was most dramatic for low and mid elevation red spruce, it was also evident for high elevation red spruce whose growth was more consistent and moderate over the length of the chronology. Interestingly, red maple also appears to be undergoing a similar increase in growth, though with a great deal of plot-to-plot variation. Little research has been devoted to red maple growth trends in the region and only a single red maple chronology (from Michigan) is archived on the International Tree Ring Data Bank (NOAA National Climatic Data Center 2014). Thus, at this time it is impossible to assess how localized this increase in red maple growth is.

Relative growth trends (1980-2012)

Trends among species

Many of the growth trends described in the previous section became more apparent when we examined standardized mean BAI (e.g., Z-score) from 1980-2012 (Figure 4). At all three low elevation plots where red maple was sampled, standardized growth was around the mean in 1980, but above the mean by 2012 (> 2 standard deviations above the mean). For sugar maple, the potential impacts of a variety of biotic and abiotic stress agents denoted in Figure 3 are evident in Figure 4 as well. Again, we see a downturn in growth coincident with the late spring frost in May 2010 that affected sugar maple at low elevation, but not as dramatically at mid elevation for either sugar maple or yellow birch. We suspect that mid elevation trees were unaffected due to a later timing of bud break relative to frost exposure. Sugar maple, at both low and mid elevations, began with higher than average growth in the 1980s and had below-average growth by the end of the chronology.

For red spruce, standardized growth began below the mean in 1980 and finished well above it in 2012 for all nine plots (Figure 4). Aside from the high elevation plot in the Stevensville Brook watershed, red spruce underwent an upswing in recent growth. Growth for red spruce at the Stevensville Brook high elevation plot was very low and uniform, with little year-to-year variation. However, this plot was not representative of red spruce in the region or even red spruce growing at other high elevation sites (Kosiba et al. 2013). Based on the similar approximate age (based on tree-ring counts) of red spruce and balsam fir trees, it is evident that the site went through a stand replacing disturbance in the early 20th century, likely logging or fire (Cogbill 1996). Whatever the cause, it now appears that this stand may be undergoing a period of stem exclusion, as was indicated by the high mortality detected in the subplot data (Table 3). Despite this, at all three high elevation plots, red spruce was growing relatively faster than balsam fir for the last decade or so. Balsam fir, on the other hand, appeared to have experienced some recent decreases in growth compared to its average for this time period. Figure 5 shows average standardized BAI for all plots by

species. For the last year of data (2012), the only species with below average growth was balsam fir. Both red spruce and red maple had high standardized BAI for that year: 2.36 and 2.86 standard deviations above the overall mean, respectively.
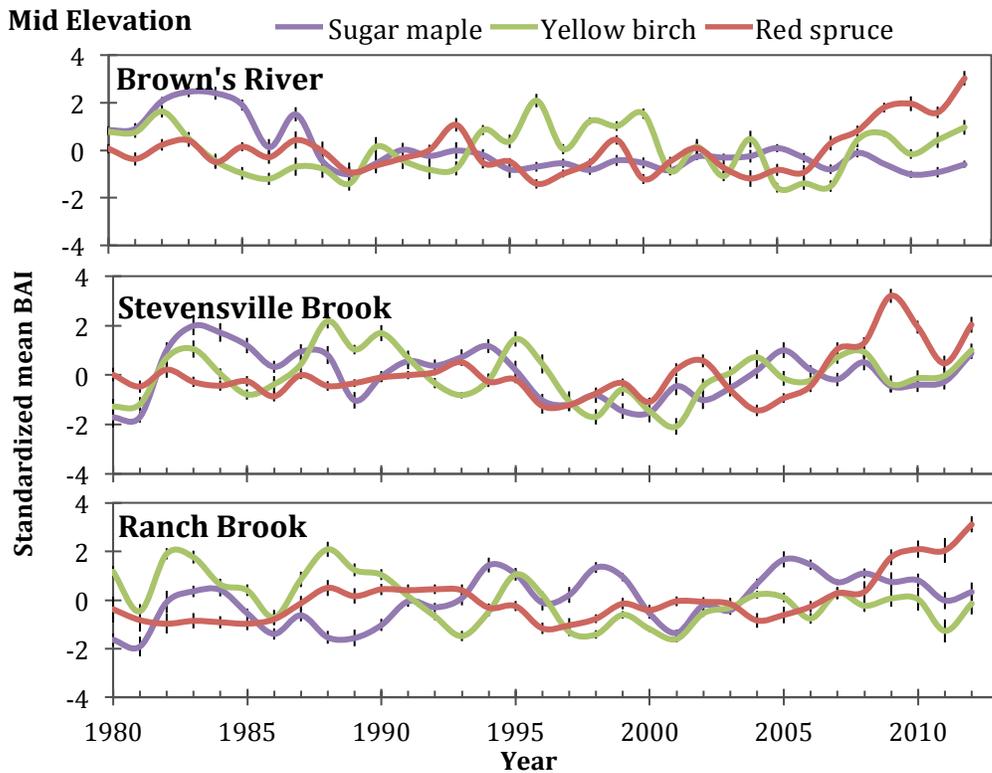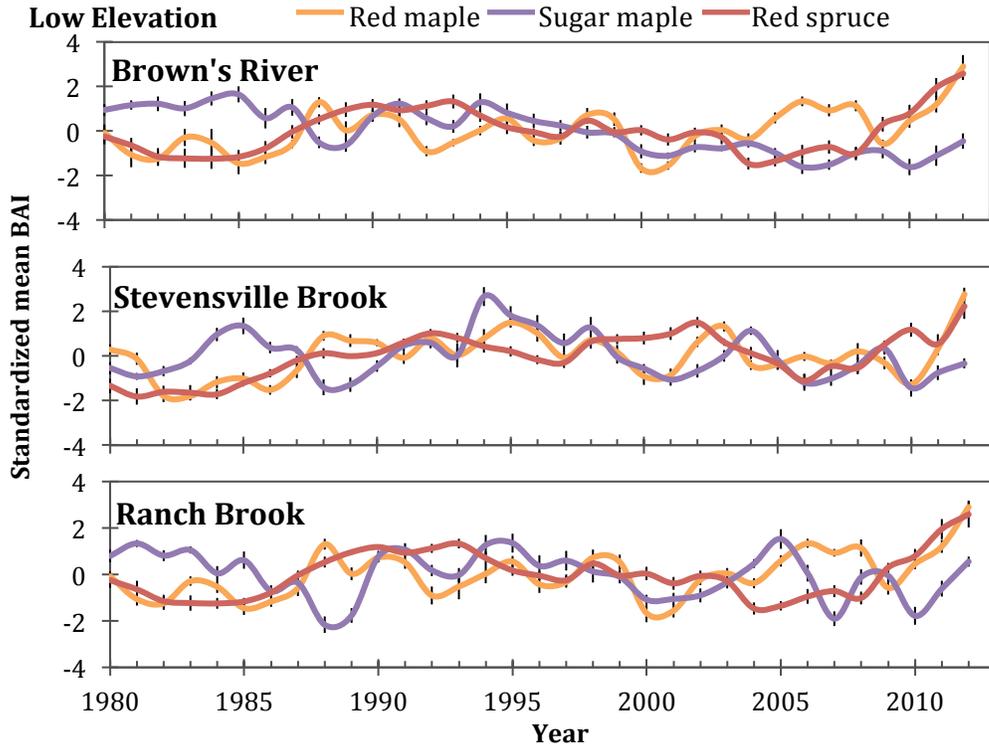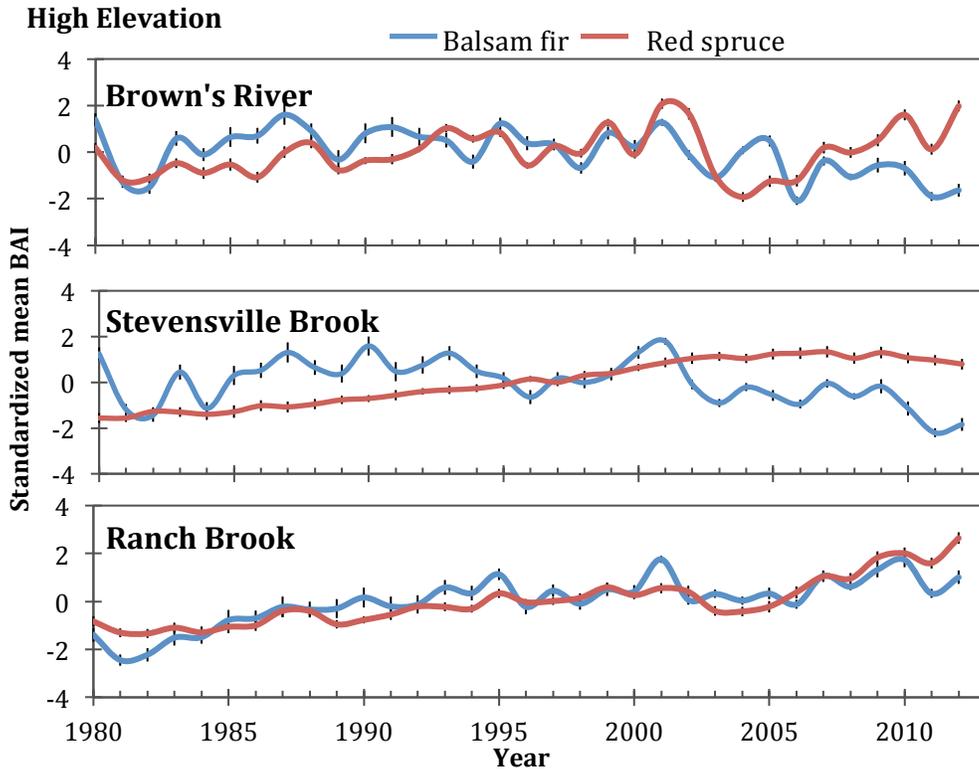
Figure 4: Standardized mean basal area increment (BAI ± SE) per plot per species per elevational zone (low < 760, mid 760-880, and high > 880 m asl) using the equation $Z = \frac{y_i - \chi}{\sigma}$ (where y_i is the mean BAI in year i, and χ and σ are the grand mean and standard deviation, respectively, for the common period [1980-2012]).
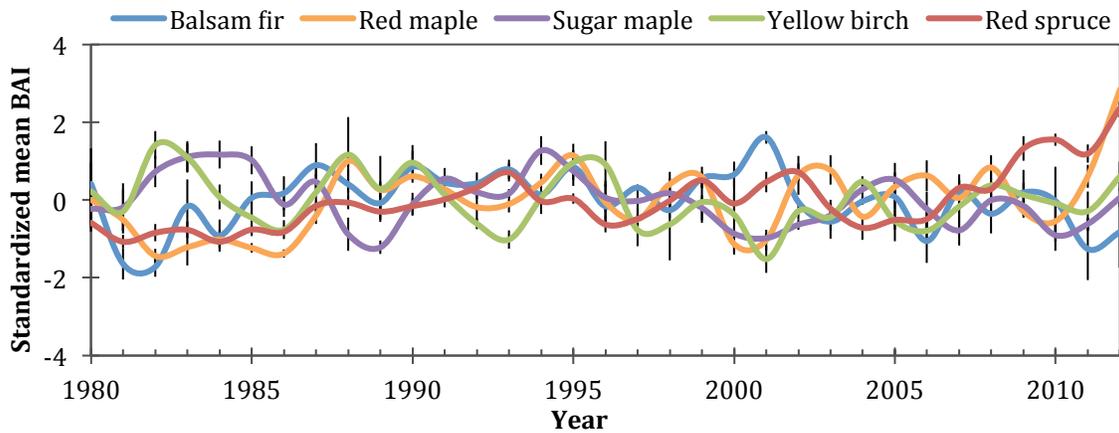

Figure 5: Standardized mean basal area increment (BAI ± SE) per species per plot using the equation $Z = \frac{y_i - \chi}{\sigma}$ (where y_i is the mean BAI in year i, and χ and σ are the grand mean and standard deviation, respectively, for the common period [1980-2012]) and averaged over all plots by species.

Trends among watersheds and elevations

When standardized growth was examined by watershed, all three watersheds had growth above the mean (from 1980-2012) in 2012 (Figure 6A), the year of sampling, driven by the recent high growth of red maple and red spruce. Overall, the watersheds exhibited similar relative growth trajectories over the 32-year period. Synchronous declines in growth in 1981 and 1989 for the three watersheds was likely due to the severe droughts that occurred then (Dupigny-Giroux 1999). Though the ice storm in 1998 negatively affected individual trees on Mt. Mansfield (Wilmot 1998), it does not appear that it drastically decreased relative growth across the watersheds. However, documented hardwood decline in 1999 combined with the effects of the 1998 ice storm may have prompted declines in growth seen in 2000 for Ranch Brook and Stevensville Brook watersheds. The similar relative growth patterns of the three watersheds are noteworthy, considering that these watersheds have different disturbance histories, relative species composition, and aspects, among other differences, but was not unanticipated since the stand-level signal captured in the mean chronology per species should represent response to weather patterns and other broad-scale environmental variables that would be similar across the watersheds.

Like the three watersheds, the three elevation zones also exhibited growth above the mean in 2012 (Figure 6B). At the beginning of the chronology in 1980, the three elevational zones had dissimilar growth trends, with high elevation plots exhibiting a decline, mid elevation showing an increase, and low elevation remaining indistinguishable in growth relative to the mean. After 1986, the three elevation zones follow similar trajectories, aside from an increase in growth in 2001 for the high elevation plot that is of unknown cause. The declines in relative growth for the low and mid elevation plots concurrent with the increase at high elevations may be a result of the 1998 ice storm and

followed by the 1999 drought. Based on figure 6B, it does not appear that the 1998 ice storm negatively affected high elevation plots.
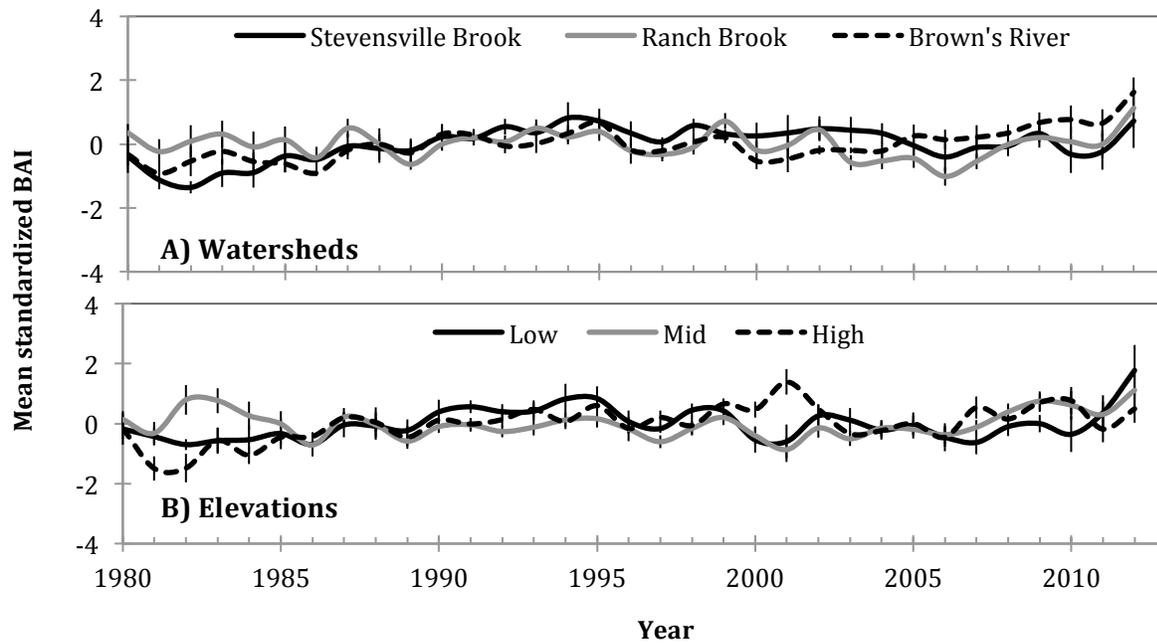

Figure 6: Standardized basal area increment (BAI ± SE) created using the equation $Z = \frac{y_i - \chi}{\sigma}$ (where y_i is the mean BAI in year i, and χ and σ are the grand mean and standard deviation, respectively, for the common period [1980-2012]) and averaged by (A) watershed (Stevensville Brook, Ranch Brook, and Brown's River) and (B) elevational zone (low < 760, mid 760-880, and high > 880 m asl) on Mt. Mansfield.

Recent relative growth trends prior to sampling (2008-2012)

<u>Differences among species</u>

Examining recent growth for the past five years (2008-2012), red spruce had significantly higher standardized growth than sugar maple, balsam fir, and yellow birch, but not red maple ($P < 0.0001$, Figure 7). Red maple had significantly higher growth than both sugar maple and balsam fir. When we tested recent growth by species to see if recent growth differed from the mean of zero, we found that for red maple ($P < 0.03$), sugar maple ($P < 0.002$), and red spruce ($P < 0.001$) recent mean growth was significantly different from zero. Since these were standardized values, with a mean of zero for the time period 1980-2012, this indicated that both red maple and red spruce were growing better than average

for this time period, while sugar maple was growing less than average, and balsam fir and yellow birch were not growing differently from their 32-year mean.
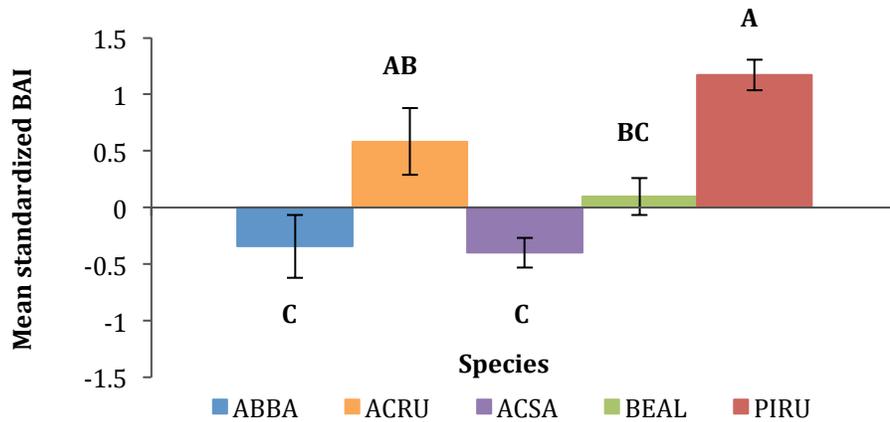

Figure 7: Mean standardized basal area increment (BAI ± SE) per species for the five years of growth (2008-2012) previous to sampling. Different letters denote significant differences (ANOVA followed by Tukey-Kramer multiple comparisons). Species codes are: ABBA, *Abies balsamea* (balsam fir); ACSA, *Acer saccharum* (sugar maple); ACRU: *A. rubrum* (red maple); BEAL, *Betula alleghaniensis* (yellow birch); and PIRU, *Picea rubens* (red spruce) (NRCS 2014). ACRU, ACSA, and PIRU differed significantly from zero, while ABBA and BEAL did not.

Differences among watersheds and elevations

When we examined standardized BAI for recent years (2008-2012), we found that all three watersheds had tree growth greater than the mean (i.e., BAI > 0); however, only Stevensville Brook and Ranch Brook were significantly greater than zero ($P < 0.04$ and $P < 0.0001$, respectively). Surprisingly, we did not find differences among elevations ($P < 0.2$), though all three elevational zones had mean standardized BAI for 2008-2012 greater than zero, but it was only significantly different for high and mid elevational zones ($P < 0.03$ and $P < 0.0001$, respectively).

There were also significant differences between watersheds ($P < 0.05$) with Brown's River (0.71 ± 0.16 [mean standardized BAI (2008-2012) ± SE]) having higher relative growth than Ranch Brook Watershed ($P < 0.05$; 0.14 ± 0.18) and Stevensville Brook (0.29 ±

0.16) being intermediate. Both Brown's River and Stevensville Brook Watersheds differed significantly from a mean of zero ($P < 0.0001$ and 0.04, respectively) (Figure 4). By plot this was driven by a significant difference in recent standardized BAI for the high elevation plots for Brown's River compared to Ranch Brook; all other plots were intermediate and not significantly different ($P > 0.06$).

There were no significant differences by elevation for standardized mean BAI over the past five years (2008-2012), though the trend was for lower elevation plots to have slightly lower values. Growth at all three elevational zones was above the mean in recent years (2008-2012) suggesting that environmental conditions in those years were more favorable to radial growth. However, these trends may have been dominated by the high growth in those same years for red maple and red spruce, both of which had mean growth greater than the 32-year average.

Climate and deposition drivers of growth

Using a linear model of standardized growth among species, we found significant differences due to both species ($P < 0.03$) and year ($P < 0.0001$), as well as an interaction between species and year ($P < 0.0001$) (Overall model $P < 0.0001$, adjusted $R^2 = 0.46$). These differences are consistent with the divergent ecological niches of the five species, though little research has been done to specifically evaluate the differential responses of these species to climate and other drivers of growth via direct comparisons under controlled conditions.

For our ANOVA model using red spruce standardized growth, we found a significant effect of year ($P < 0.0001$) and elevation ($P < 0.0001$, adjusted $R^2 = 0.70$), with year and the interaction between year and elevation being significant ($P < 0.0001$) (Figure 8). All three elevations displayed a dip in growth concurrent with the 2003 winter injury event and verify growth reductions thereafter (Kosiba et al. 2013), as well as a strong increase in growth since then (Figure 8). We found that our model accounted for 56% of the variation in growth ($P < 0.0001$, adjusted $R^2 = 0.56$).
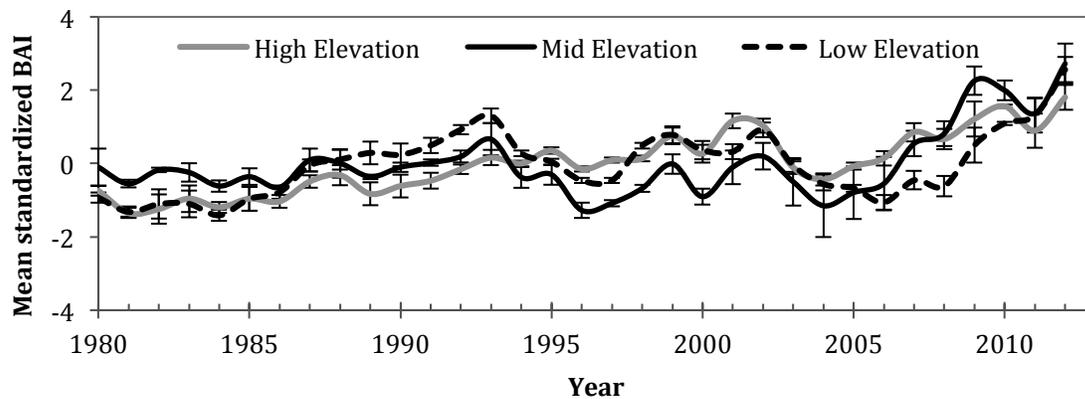

Figure 8: Mean standardized basal area increment (BAI ± SE) for red spruce trees (*Picea rubens*) at the three elevational zones (low < 760, mid 760-880, and high > 880 m asl) on Mt. Mansfield.

To evaluate differential growth among the species over time, we compared growth with various environmental factors (e.g., temperature, precipitation, deposition, etc.) that may help drive year-to-year differences and the interaction between year and species. We added select parameters identified using PCA analysis to a stepwise linear regression. Table 2 lists the significant parameters associated with species-specific growth. Both balsam fir and yellow birch show relatively few associations of growth with the selected environmental parameters; the parameters positively associated with growth increases were previous February maximum temperature and [H+] deposition, respectively. The general lack of association with environmental parameters here suggests that these species

are primarily responding to variables (e.g., succession and stand dynamics, other weather

parameters, soil moisture, etc.) that were not considered in this analysis.

Table 2: Species-specific stepwise linear regression using standardized BAI per species (1980-2012) and environmental parameters. Principal Components Analysis (PCA) was used to narrow down influential climate and deposition parameters to be added to stepwise linear regression. Only parameters with significant results are shown.

Species	Term	Association with growth	Prob > |F|
Red maple	Mean summer temperature	+	0.0005
	January maximum temperature	+	0.0007
	July minimum temperature	+	< 0.0001
	Previous February minimum temperature	-	0.02
	Atmospheric [CO_2]	+	0.01
	Cation:anion deposition	+	< 0.0001
	NH_4:SO_4 deposition	+	< 0.0001
Sugar maple	Previous March maximum temperature	-	0.009
	Previous Nov maximum temperature	-	0.03
	January Maximum temperature	-	< 0.0001
	Previous November minimum temperature	-	0.0006
	January total precipitation	+	0.005
Balsam fir	Mean annual precipitation	-	< 0.0001
	[H+] deposition	+	0.05
Yellow birch	Previous February maximum temperature	-	0.01
	March Mean Temperature	+	0.01
Red spruce	Previous February total precipitation	+	0.004
	Cation:anion deposition	+	< 0.0001
	Growing degree days (GDD)	+	0.005
	NH_4:SO_4 deposition	+	< 0.0001

Especially striking when compared to red spruce and red maple, sugar maple had

only one parameter that had a positive relationship with growth, with the other four being

negative. Surprisingly, all but one of these parameters occurred in the winter months, which

according to climate projections could be the season to experience the most change in our

region (IPCC 2014). Sugar maple growth was negative related to maximum winter

temperatures, perhaps because these parameters are associated with low snow pack which

has been shown to cause growth declines and root damage due to increased soil frost depth
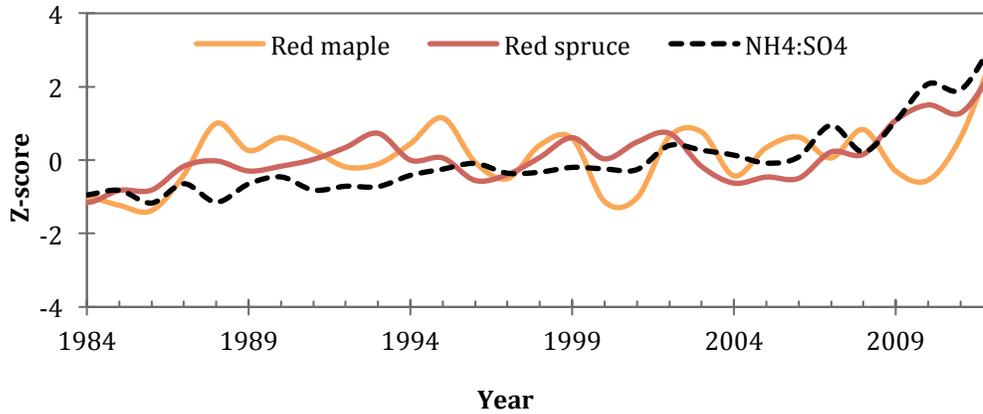
(Comerford et al. 2013).

Figure 9: Standardized red maple and red spruce basal area increment (BAI) and precipitation-weighted means (mg/L) for ammonium (NH_4^+) relative to sulfate (SO_4^{2-}) deposition ($NH_4:SO_4$) for Mt. Mansfield (Underhill, VT) from 1984-2012 (National Atmospheric Deposition Program 2014). Standardized (Z-scores) were generated using the equation $Z = \frac{y_i - \chi}{\sigma}$ (where y_i is the mean in year i, and χ and σ are the grand mean and standard deviation, respectively).

We found that ammonium (NH_4^+) to sulfate (SO_4^{2-}) ($NH_4:SO_4$) and cation to anion deposition ratios were both positively associated with red spruce growth since 1980 (Table 2, Figure 9). Both of these trends are consistent with the well-documented sensitivity of red spruce to pollution inputs (DeHayes et al. 1999). Red spruce growth could be positively associated with higher ratios of cations over anions in deposition because acid inputs deplete Ca from forests and that loss predispose red spruce to foliar winter injury and associated growth declines (Schaberg et al. 2010, Kosiba et al. 2013). Indeed, when we looked at the linear relationship between red spruce growth and $NH_4:SO_4$, the two had an adjusted R^2 of 0.61 ($P < 0.0001$), however, when years of known winter injury in the region (see Lazarus et al. 2004) were removed from analysis, the adjusted R^2 increased to 0.68 ($P < 0.0001$) indicating that the relationship between growth and $NH_4:SO_4$ was lessened by the occurrence of winter injury events. Deposition of $NH_4:SO_4$ could also be positively related to red spruce growth since a higher $NH_4:SO_4$ ratio may allow NH_4^+ to act as a fertilizer in systems that are nitrogen limited, while reduced SO_4^{2-} limits its availability to act as a

counter ion that fosters Ca leaching and depletion. Though sulfur deposition was once a

significant component of acid deposition that contributed to red spruce decline (DeHayes et

al. 1999), it has declined in the region since the enactment of amendments to the Clean Air

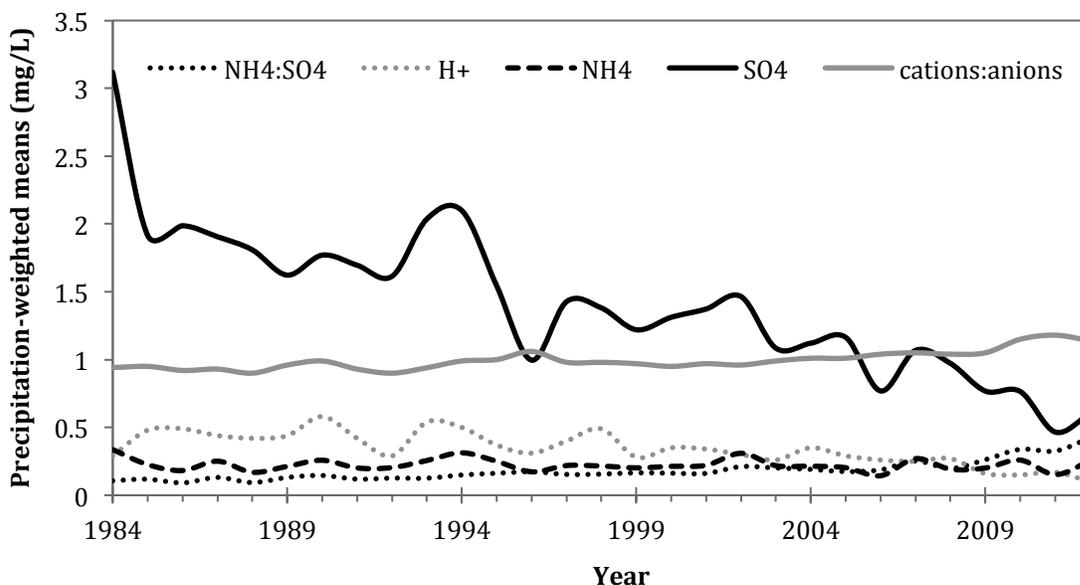Act in 1990 (Greaver et al. 2012) (Figure 10).

Figure 10: Precipitation-weighted means (mg/L) for ammonium (NH_4^+), sulfate (SO_4^{2-}), hydrogen ions (H^+), and the ratios between NH_4:SO_4 and cations:anions for Mt. Mansfield (Underhill, VT) from 1984-2012 (National Atmospheric Deposition Program 2014).

Also since red spruce is a temperate conifer that can photosynthesize in spring and

fall provided that temperatures are moderate (Schaberg and DeHayes 2000), it has been

hypothesized that the recent upsurge in growth for this species could be due to climate

warming that has lengthened the functional growing season (Kosiba et al. 2014). Indeed,

regression analysis for red spruce growth on Mt. Mansfield and growing degree days data

show support for this hypothesis (Table 2). The number of growing degree days for

Burlington, VT have increased 26% since 1980 ($P < 0.003$, adjusted $R^2 = 0.23$).

Like red spruce, red maple also appears to be experiencing a period of increased growth – though this preliminary interpretation is based on a much smaller sample size. At this time, it is unclear if this is a limited phenomena or a region-wide increase as it is for red spruce. Like red spruce, red maple also showed a significant positive relationship with NH_4:SO_4 and cation:anion deposition (Table 2, Figure 9). Since red maple has been much less studied in terms of relationships with acidic inputs and deposition, we can only hypothesize that similar mechanisms may be at play with red maple. Red maple also shows a positive relationship with atmospheric CO_2 concentration, which other research has shown may result in a fertilization effect for trees, though studies have had varied results (Hattenschwiler et al. 1997, Soule and Knapp 2006). Mohan et al. (2004) detected a fertilization effect of elevated CO_2 concentrations for red maple seedlings, but also found a high degree of variability in response. Since red maple was only sampled at low elevations, we also do not to know if elevation plays a role in this species' growth increase. Growth increases for red maple could have a large effect on the forests in the region because it is one of the most abundant trees in New England and has a large ecological amplitude (Abrams 1998).

Comparisons with other chronologies

We compared red spruce growth from this study with red spruce growing at a wide range of plots in Vermont, New Hampshire, and Massachusetts (*N* trees = 452) collected in 2010, 2011, and 2012 (Weverka 2012, Engel 2013, Kosiba et al. 2013). A linear regression resulted in a significant relationship between the two chronologies (P < 0.0001, adjusted R^2 = 0.84; Figure 11A). It is clear that red spruce growth at the Mt. Mansfield study plots correspond well with red spruce growth region-wide.

We constructed an ANOVA model to examine if there were differences in BAI growth between the Mt. Mansfield and regional chronologies. We found a significant effect of year ($P < 0.0001$) and location (Mt. Mansfield vs. Region, $P < 0.0001$), but no interaction between year and location ($P > 0.98$) indicating that while there are differences between the chronologies in any given year, the two are responding similarly over time. When we looked at individual year differences, the only years that were significantly different between the two chronologies were 1998 ($P < 0.04$), 1999 ($P < 0.02$) and 2003 ($P < 0.02$). Interestingly, the differences in growth for those years could be explained by the variable effects of abiotic factors and subsequent decline thereafter: an ice storm in 1998, drought in 1999, and winter injury in 2003. All of these events were reported for some of these plots based on over-flight images and written reports (Wilmot 1998, Lazarus et al. 2004, Vermont Agency of Natural Resources Department of Forest Parks & Recreation 2013) and had a variable effect across the landscape due to a combination of aspect and elevation. Perhaps the spatial variability of damage from these events resulted in the temporary de-coupling of Mt. Mansfield and regional chronologies in these years.

It is interesting that the period of most divergent growth between Mt. Mansfield and regional red spruce is the period from roughly 1980 through 2008 – a period interspersed with a series of winter injury events with varied intensities and legacies across the region (Lazarus et al. 2004, Kosiba et al. 2013). The regional chronology would provide the best estimate of broad-scale impacts from these winter injury events. The better than average growth at Mt. Mansfield relative to the regional chronology could indicate that red spruce on Mt. Mansfield were, on average, injured less than the regional norm.

We also compared sugar maple and yellow birch from this study to those species sampled from the Hubbard Brook Experimental Forest (HBEF) in 2012 (Hansen in prep). For sugar maple (N trees HBEF = 163; Figure 11B) the two chronologies were significantly

related ($P < 0.0001$, adjusted $R^2 = 0.41$). Looking at the two chronologies in a linear ANOVA model using year, location (HBEF vs. Mt. Mansfield), and the year x location interaction as sources of variation, we found a significant effect of both year and location on growth ($P < 0.0007$ and 0.0001, respectively), but no interaction of the two ($P > 0.7$). Sugar maple growing in HBEF had significantly higher growth than those at Mt. Mansfield ($P < 0.0001$), with significant years of difference being: 1950-52, 1954-55, 1957-58, 1960-61, 1963, 1967-68, 1970-82 ($P \leq 0.05$ for all). After 1982, the two chronologies were not significantly different in any year. Both chronologies show a decline in growth in the late 1980's, which aligns with other reports of sugar maple declines in BAI at that time (Duchesne et al. 2003, Long et al. 2009).

Sugar maples also appear to be fairly constant in growth, although perhaps slightly in decline concurrent with other locations (Duchesne et al. 2003, Long et al. 2009). However, at HBEF, sugar maple growth has declined precipitously since the early 1980s to growth rates comparable to those at Mt. Mansfield. Growth declines evident for sugar maple in the 1980s (Figure 11B) coincided with a period of regional decline for the species that was attributed to the combined effects of acid deposition-induced Ca depletion and the influences of various secondary stressors (Horsley et al. 2000, Duchesne et al. 2003, Huggett et al. 2007, Long et al. 2009). The decline of trees at HBEF resulted in lower levels of growth that have long been the norm for sugar maples at Mt. Mansfield (Figure 11B). From these data, it is unclear why sugar maple at HBEF would have begun the first part of the chronology with higher growth than those at Mt. Mansfield, but perhaps the effects of acidic deposition occurred earlier than at HBEF do to the west-east pattern of deposition.
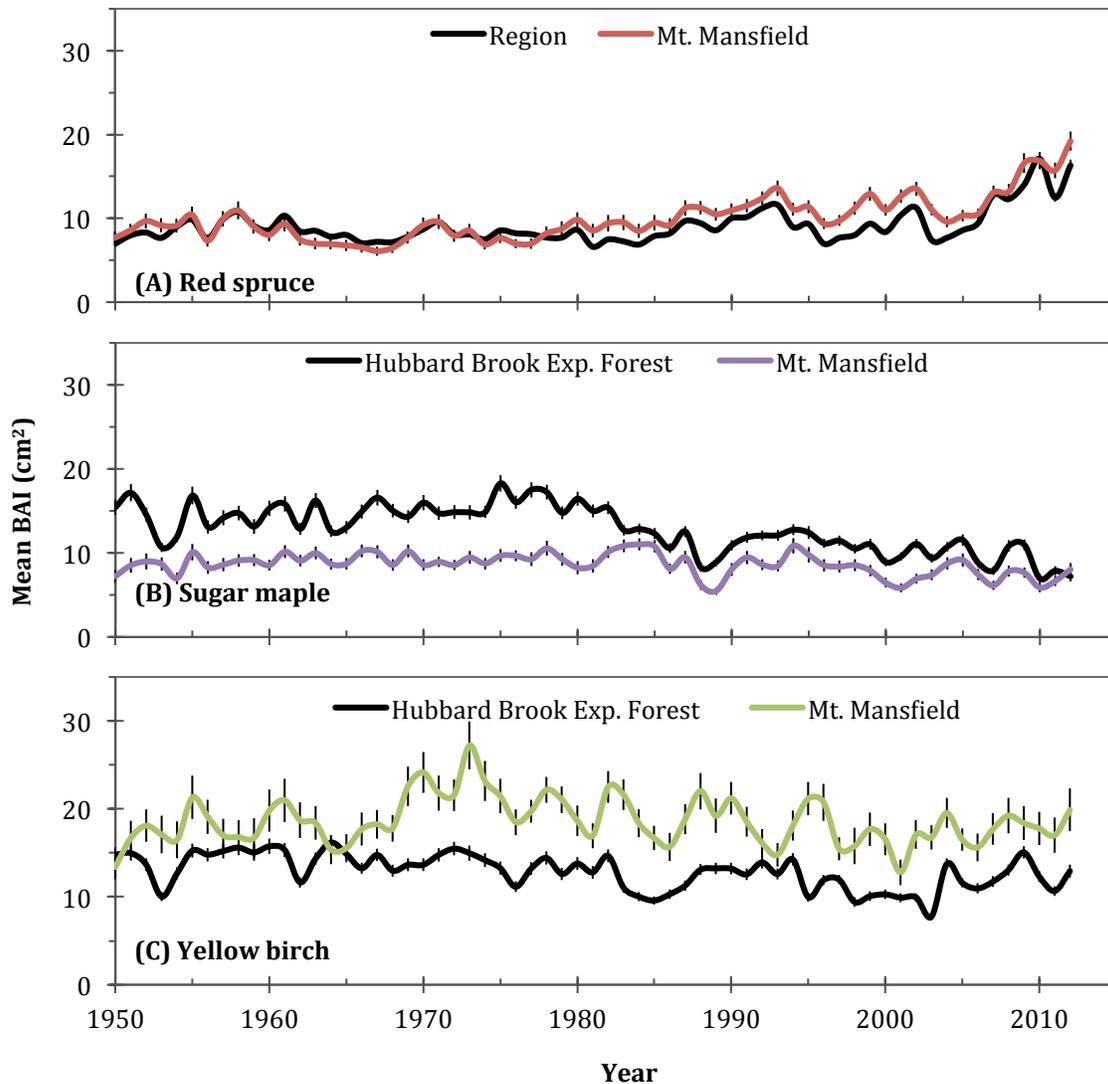
Figure 11: Chronologies (BAI ± SE) from 1950-2012 for (A) red spruce (red line) from this study on Mt. Mansfield and the wider region (black line) (includes plots from Vermont, New Hampshire, and Massachusetts); (B) sugar maple (purple line) from this study on Mt. Mansfield and Hubbard Brook Experimental Forest, New Hampshire (black line); and C) yellow birch (green line) from this study on Mt. Mansfield and Hubbard Brook Experimental Forest, New Hampshire (black line).

However, to support this hypothesis, for sugar maple at Mt. Mansfield one would expect to see a precipitous decline in growth earlier in the chronology than the one seen at HBEF; but growth appeared steady over the length of the chronology (Figure 3). Another

possibility is that Mt. Mansfield is a more marginal site for sugar maple growth compared to HBEF and therefore baseline growth rates were lower at Mt. Mansfield relative to HBEF.

For yellow birch (N trees HBEF = 170; Figure 11C) the similarity of growth relationships between Mt. Mansfield and HBEF was not as strong as for the red spruce and sugar maple chronologies, though the yellow birch chronologies were still significantly related ($P < 0.02$, adjusted $R^2 = 0.077$). One possible reason for the weaker relationship between Mt. Mansfield and HBEF yellow birch compared to that detected for sugar maple could be the lower sample size for birch ($N = 34$ trees) relative to sugar maple ($N = 63$ trees) at Mt. Mansfield. A lower sample size could reduce the accuracy of yearly growth mean estimates and increase the variation around those means (i.e., SEs for Mt. Mansfield trees in Figure 11C), both of which could complicate trend analysis. These results demonstrate the importance of having high replication when looking at region-wide patterns in tree cores. A small sample size and limited spatial scale results in chronologies that can be more dominated by local forces.

Examining the two yellow birch chronologies in an ANOVA model, only year was a significant source of variation ($P < 0.01$). Location ($P > 0.7$) and the interaction between year x location ($P > 0.9$) were not. Significant years of difference were 1953, 1955, 1962, 1969-79, 1982-1985, 1987-88, 1990-91, 1995-96, 1998-2000, 2002-03, 2008, 2011-12 ($P < 0.05$ for all). Because we had relatively few trees for the yellow birch chronology ($N = 34$), the lack of relationship with yellow birch growing at HBEF may indicate that the former chronology was driven by site-specific factors (also evident by the large standard error bars around the means which indicate large variation in response among trees and watersheds). While yellow birch in this study contained a high degree of between-watershed and between-year variation, the trees have remained fairly constant in their growth over time at Mt. Mansfield and when compared to HBEF.

The specifics of harvest cycles and land use changes at Mt. Mansfield could combine to create tree growth and succession cycles that were divergent from the region as a whole. Despite this possibility of divergence, when the tree ring chronologies from Mt. Mansfield were compared to others from the region, several similarities emerged. For red spruce, this alignment between patterns of growth for Mt. Mansfield and the region was quite striking (Figure 11A). Indeed, the similarity of response across locations and years suggests that broad-scale factors (i.e., climate or regional pollution inputs) are the primary drivers of growth for red spruce, rather then more localized disturbance patterns. We are currently investigating larger-scale evaluations of red spruce growth to environmental parameters. The similarities in overall and year-to-year variation in growth for sugar maple and yellow birch at Mt. Mansfield and HBEF further highlight the likelihood that broad factors (e.g., climate or regional pollution inputs) are driving the growth of these species. It would also be interesting to examine how growth of balsam fir and red maple compare to regional chronologies; however, there are currently few chronologies of these species available for comparison.

Proxies for tree growth

Sapwood area

Sapwood area (cm^2) for the two conifers, balsam fir and red spruce, was significantly related to both tree vigor rating (inversely related, P < 0.0001 for both species, Wilcoxon Nonparametric test, results not shown) and mean BAI (Red spruce: P < 0.0001, adjusted R^2 = 0.64; balsam fir P < 0.0001, adjusted R^2 = 0.27; Figure 12) for the past five years (2008-2012). This aligns with other studies that have shown a strong relationship of sapwood area with foliar biomass and total basal area (Grier and Waring 1974, Kendall Snell and Brown 1978).
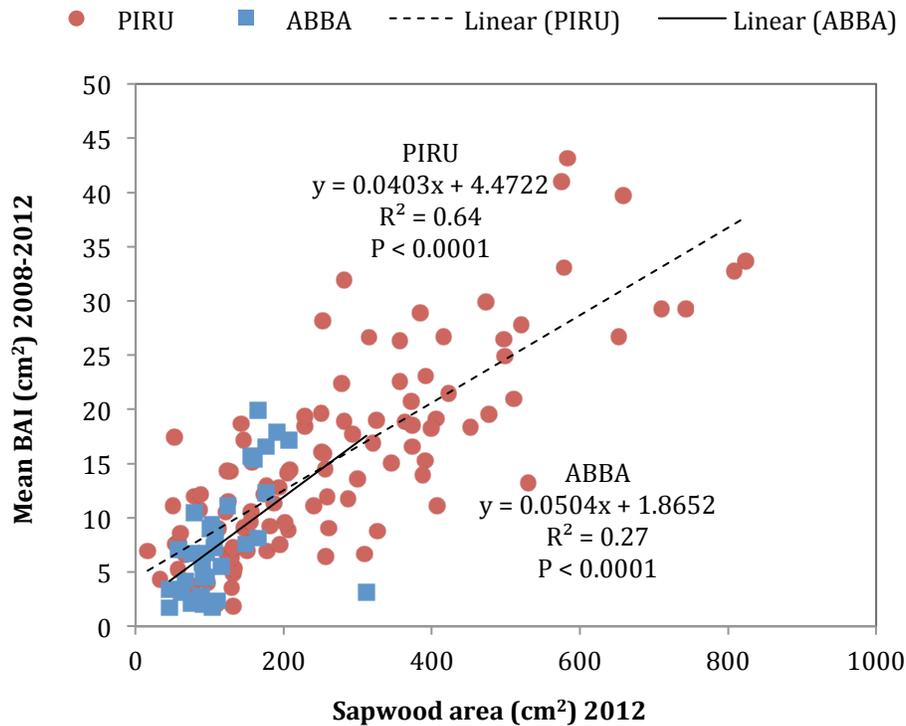
Figure 12: Mean sapwood area (cm², assessed in 2012) per tree regressed with mean basal area increment (BAI ± SE) from 2008-2012 per tree for balsam fir (*Abies balsamea,* ABBA) and red spruce trees (*Picea rubens*, PIRU) on Mt. Mansfield. For both species, there was a significant linear relationship between sapwood area and recent BAI ($P < 0.0001$ for both species).

Sub-plot basal area

Mean stand basal area for all plots was 30.9 ± 2.4 m² ha⁻¹. Subplot total basal area did not differ by elevational zone ($P > 0.5$), but it did significantly differ by watershed ($P < 0.008$)(ANOVA), with Stevensville Brook watershed plots containing significantly more total basal area (40.9 ± 3.7 m² ha⁻¹) than either Brown's River (26.8 ± 3.8 m² ha⁻¹) or Ranch Brook (24.3 ± 4.0 m² ha⁻¹) watersheds, which were not significantly differ from each other ($P< 0.03$ and 0.01, respectively; Tukey-Kramer HSD). This was driven by the significant difference in basal area per plot ($P < 0.02$, Table 3). The Stevensville Brook mid elevation plot had significantly greater basal area than both the mid elevation plots in either Brown's

River or Ranch Brook Watersheds ($P < 0.05$ and 0.02, respectively). The Stevensville Brook

high elevation also has a high number of sub-plot trees with a vigor rating of 5 (i.e., dead).

Table 3: Mean (± SE) basal area (m^2 ha^{-1}) based on four to six 24-ft radius subplots per plot. In each subplot, all woody stems > 12.7 cm (> 5.0 in) DBH were measured. Watersheds were significantly different in basal area ($P < 0.05$), while elevational zones (low < 760, mid 760-880, and high > 880 m asl) were not ($P < 0.5$). Individual plots significantly differed in basal area ($P < 0.02$). Different letters denote significant differences in basal area (ANOVA with Tukey-Kramer HSD). Pie charts depict ratio of vigor rating for woody stems in sub-plots (with a vigor of 1 being healthy and 5 being dead). There was a significant difference in vigor rating ratios among plots ($P < 0.0001$), elevations ($P < 0.0001$), and transects ($P < 0.0001$)(Chi square).

Watershed	Elev. category	Mean basal area (m^2 ha^{-1}) ± SE	Vigor rating ratios per sub-plot
Brown's River Watershed[a]	Low	29.3 ± 6.6[AB]	
	Mid	21.1 ± 6.6[B]	
	High	31.4 ± 3.0[AB]	
Ranch Brook Watershed[b]	Low	26.8 ± 4.6[AB]	
	Mid	13.7 ± 3.3[B]	

	High	31.2 ± 7.8[AB]	
Stevensville Brook Watershed[b]	**Low**	30.3 ± 2.5[AB]	
	Mid	48.8 ± 10.8[A]	
	High	44.8 ± 6.6[AB]	
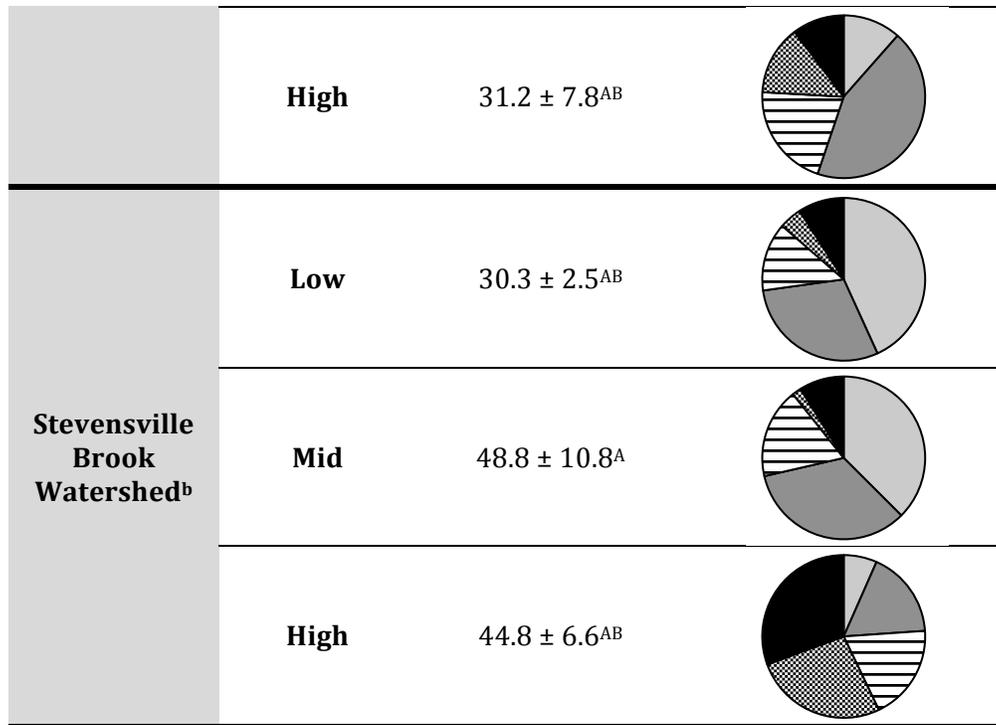
Tree vigor & dieback

Tree vigor alone was a moderate indicator of either 2012 growth ($P > 0.06$; not shown) or an average of 2008-2012 growth ($P > 0.06$; Figure 13) for all trees in this study. Although there was a trend for trees in vigor classes 1 and 2 (i.e., "healthy") to have higher growth than those in 3 and 4 (i.e., "declining"), a pairwise test did not detect significant differences. Looking at species, this lack of a relationship may have been driven by the fact that 97% of yellow birch and 92% of sugar maple were rated as 1 or 2 for vigor. Red maple, the species with trees in all four vigor categories, did not have a significant relationship with vigor rating and growth ($P > 0.7$), whereas balsam fir and red spruce did. For balsam fir, vigor class 1 was significantly higher in growth than the other three classes ($P < 0.0001$). For red spruce, both vigor classes 1 and 2 were significantly different from 4, with 3 being intermediate ($P < 0.0001$). Because of the low sample sizes for some vigor classes, we did not include vigor rating in our linear models examining the possible drivers for growth patterns. Vigor rating was not significantly related to crown class.
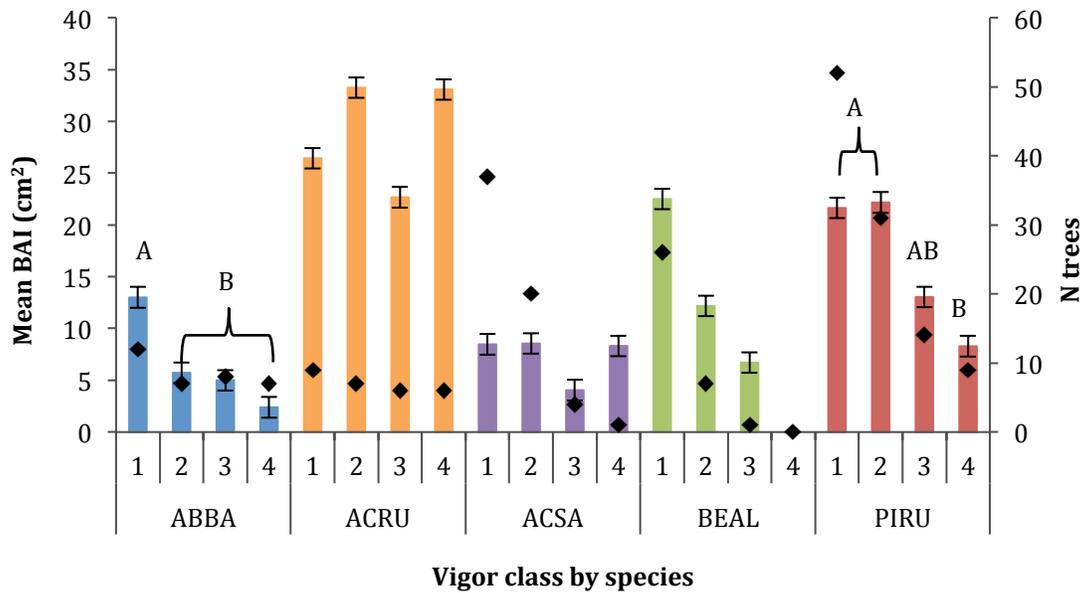
Figure 13: Mean basal area increment (BAI ± SE) for the five years before sampling (2008-2012) per vigor class by species (colored bars; with vigor 1 being healthy and 4 being in decline). Number of trees contributing to each mean shown on z-axis (black diamonds). By species, only PIRU and ABBA had significant differences between BAI and vigor rating (*P* < 0.0001 for both species; vigor classes with different letters were significantly different within species; ANOVA followed by Tukey-Kramer multiple comparisons). Species codes are: ABBA, *Abies balsamea* (balsam fir); ACSA, *Acer saccharum* (sugar maple); ACRU: *A. rubrum* (red maple); BEAL, *Betula alleghaniensis* (yellow birch); and PIRU, *Picea rubens* (red spruce) (NRCS 2014).

Species comparisons

Our comparative analysis detected significant differences in growth relationships among species over time. The five species evaluated had different overall growth rates that were not predictable based on physiological characteristics or elevation alone. None of the five species in this study appear to be in drastic decline, though the recent growth of sugar maple was significantly less than its 32-year mean (Figure 6). Balsam fir also had lower than average growth for recent years, though it was not significantly different from the mean.

Overall, red maple growth on Mt. Mansfield was quite high. Even trees with poor vigor ratings (i.e., rating of 3 or 4) had similar or higher growth during the past five years

than trees of other species rated at vigor class 1 (Figure 13). When red maple growth is standardized by it's own growth since 1980, it has grown significantly more in the past five years (Figure 6). Reports have shown that red maple abundance has increased since the 20th century (Siccama 1971) . Red maple has been called a "super-generalist" since it is a species with low resource requirements and a large ecological amplitude because it is found on a range of site conditions, from wet to dry and sunny to shady (Adams 1998). Although red maple suffered a period of decline in the late 1970's (Figure 3), by the late 1980s these trees had surpassed previous growth rates.

Red spruce have experienced a well-documented decline since the mid-twentieth century that was instigated by high acid loading (e.g., DeHayes et al. 1999). However, this work and others have shown that red spruce is now experiencing a marked upsurge in growth (Kosiba et al. 2013, C. Cogbill personal communication). On Mt Mansfield, this upsurge has occurred regardless of the elevation or watershed assessed. Red spruce trees sampled for this study align very well with other red spruce trees across the region despite the small spatial extent of the Mt. Mansfield study area. The synchronous increase in growth in recent years points to a regional phenomenon, similar to the ubiquitous decline in growth following the 2003 winter injury event. Could this be evidence of recovery from acid-deposition-mediated decline? Our preliminary analysis on the factors leading to this growth suggest that deposition rate changes, climate and other changes in the environment are all statistically associated with the recent increase in growth.

Conclusions

We presented a comparison of growth trends for five key species at the Vermont Monitoring Cooperative's long-term study site located at Mt. Mansfield State Forest in Vermont. This project has allowed us to create a baseline of growth for red maple, sugar

maple, yellow birch, balsam fir, and red spruce at three elevations and in three watersheds on Mt. Mansfield. From this baseline, changes in forest growth rates and vigor can then be evaluated – a necessary step to understanding the fluctuations in ecosystem services that may accompany changes in our climate.

Not only were we able to examine growth changes over the length of the chronologies, we also evaluated how growth responded to various environmental parameters. It appears that our hypothesis was correct: some tree species may be responding favorably to changing environmental conditions, while others are either declining or stable. Though this specific project covered a small spatial scale, it opens avenues for future studies to examine more fully some of the patterns that emerged here. Indeed, there have been relatively few studies that have examined growth trends and responses to the environment between species in the region; yet, this is of particular interest as our climate changes and the future state of forest heath and productivity remains uncertain. We are currently underway in a continued effort to examine the growth responses of some or all of these species on larger spatial and temporal scales that will help inform us if the patterns evident at Mt. Mansfield are regional as well.

Key findings

- We detected significant differences in xylem growth associated with year, elevation, watershed, and species.
- There was a large variation in mean BAI among the species, with red maple, yellow birch, and red spruce showing the greatest growth and sugar maple and balsam fir the least.
- The timing of maximum growth also varied among the species, with sugar maple and yellow birch growing best in the 1960s-80s, and red spruce and red maple showing the greatest growth only very recently.

- During the past five years, red spruce and red maple were growing significantly better, balsam fir and yellow birch were growing same, and sugar maple growing significantly worse than species-specific means since 1980.

- In contrast to the major document decline reported for the 1970s and 1980s, red spruce had the highest growth that has occurred in the last 100 years.

- Many year-to-year declines in growth were likely associated with specific stress events (e.g., droughts, spring frosts, ice storms, etc.).

- However, protracted patterns in growth (e.g., the recent upsurges in growth for red spruce and red maple) were more likely associated with broader climate or deposition trends.

- Comparisons of growth patterns for red spruce, sugar maple and yellow birch at Mt. Mansfield to datasets from elsewhere suggest that, at least for these species, growth at Mt Mansfield was similar to regional trends.

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Appendices

APPENDIX I: Plot and tree ring data listed by watershed, elevational zone, and target species. Species codes are: ABBA, *Abies balsamea* (balsam fir); ACSA, *Acer saccharum* (sugar maple); ACRU: *A. rubrum* (red maple); BEAL, *Betula alleghaniensis* (yellow birch); and PIRU, *Picea rubens* (red spruce) (NRCS 2014).

Watershed	Elev. zone	Elev. (m)	Lat, Long	Target species	N cores	N trees	Interseries correlation[A]	Mean sensitivity[A]	Mean length of series[A]	Mean ring width (± SD)[A]	Unfiltered Auto-correlation[A]	Expressed population signal[B] (with year EPS < .85)
Brown's River Watershed	**Low**	510	(44.532, -72.828)	ACRU	14	8	0.606	0.228	62.6	2.74 ± 1.01	0.71	0.92 (1944)
				ACSA	17	10	0.505	0.254	71.8	1.9 ± 0.95	0.781	0.91 (1939)
				PIRU	20	11	0.505	0.271	132.1	1.01 ± 0.74	0.871	0.92 (1895)
	Mid	760	(44.528, -72.836)	ACSA	21	12	0.456	0.323	70.9	1.42 ± 0.68	0.679	0.91 (1942)
				BEAL	22	12	0.445	0.298	92.9	1.81 ± 0.97	0.784	0.91 (1933)
				PIRU	23	11	0.505	0.255	105.5	1.2 ± 0.78	0.867	0.92 (1895)
	High	985	(44.532, -72.822)	ABBA	21	11	0.603	0.222	67.7	1.52 ± 0.59	0.749	0.94 (1937)
				PIRU	22	12	0.562	0.235	78.6	1.37 ± 0.72	0.821	0.94 (1939)
Ranch Brook Watershed	**Low**	631	(44.514, -72.809)	ACRU	14	9	0.409	0.207	57.9	2.45 ± 0.81	0.705	0.86 (1980)
				ACSA	17	9	0.436	0.343	78.5	1.49 ± 0.91	0.811	0.87 (1977)
				PIRU	21	11	0.538	0.269	144.6	1.08 ± 0.82	0.899	0.93 (1895)
	Mid	786	(44.507, -72.798)	ACSA	19	12	0.493	0.318	91.6	1.24 ± 0.68	0.749	0.92 (1922)

				BEAL	19	11	0.489	0.274	87.8	1.83 ± 0.88	0.748	0.91 (1915)
				PIRU	24	12	0.613	0.26	149.4	1.23 ± 0.75	0.857	0.95 (1985)
	High	934	(44.520, -72.812)	ABBA	20	12	0.569	0.21	77.4	1.43 ± 0.73	0.847	0.94 (1917)
				PIRU	23	12	0.552	0.237	74.2	1.31 ± 0.61	0.809	0.94 (1928)
Stevensville Brook Watershed	**Low**	454	(44.510, -72.826)	ACRU	20	11	0.528	0.241	101.4	1.44 ± 0.63	0.752	0.92 (1901)
				ACSA	14	10	0.482	0.314	99.9	1.1 ± 0.66	0.783	0.90 (1914)
				PIRU	15	9	0.514	0.23	93.7	1.24 ± 0.64	0.817	0.90 (1931)
	Mid	760	(44.506, -72.843)	ACSA	17	10	0.45	0.335	88.9	1.22 ± 0.69	0.69	0.89 (1929)
				BEAL	19	11	0.466	0.287	80.7	2.04 ± 1.01	0.731	0.91 (1928)
				PIRU	28	11	0.558	0.246	136.9	1.32 ± 0.70	0.829	0.93 (1895)
	High	922	(44.516, -72.820)	ABBA	18	11	0.576	0.194	73.1	1.15 ± 0.55	0.84	0.94 (1934)
				PIRU	33	17	0.622	0.235	79.7	1.03 ± 0.74	0.897	0.97 (1927)

[A] From COFECHA output (Holmes 1983)

[B] $EPS = (t * r_{bt})/(t * r_{bt} + (1 - r_{bt}))$ where t is the average number of trees in the series and r_{bt} is the mean series intercorrelation (Wigley et al., 1984)

APPENDIX II: Tree vigor and dieback rating scales (from Cooke et al. 1996, USDA Forest Service 2006)

Tree vigor rating scale:

1	Healthy	• Tree appears in good health • No major branch mortality • Crown is reasonably normal within stand • <10% branch/twig mortality, defoliation, or discoloration
2	Light Decline	• 10-25% crown has branch mortality, twig dieback, or foliage discoloration • <26 % crown has broken branches or missing crown area
3	Moderate Decline	• 26-50% branch mortality, twig dieback
4	Severe Decline	• >50% branch mortality, twig dieback, or discoloration • >50% of crown has broken or missing branches
5	Dead	• No live foliage
		•

Crown dieback rating classification scale:

Class Code	Class Range
0	0
5	1-5
10	6-10
15	11-15
20	16-20
25	21-25
30	26-30
35	31-35
40	36-40
45	41-45
50	46-50
55	51-55
60	56-60
65	61-65
70	66-70
75	71-75
80	76-80
85	81-85
90	86-90
95	91-95
99	96-99
100	100