ARTICLE

Comparative growth trends of five northern hardwood and montane tree species reveal divergent trajectories and response to climate

Alexandra M. Kosiba, Paul G. Schaberg, Shelly A. Rayback, and Gary J. Hawley

Abstract: In the northeastern United States, tree declines associated with acid deposition induced calcium depletion have been documented, notably for red spruce (*Picea rubens* Sarg.) and sugar maple (*Acer saccharum* Marsh.). There is conflicting evidence concerning whether co-occurring tree species capitalized on these declines or suffered similar growth reductions and on how growth has fluctuated relative to environmental variables. We examined five species along three elevational transects on Mt. Mansfield, Vermont: sugar maple, red spruce, red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), and balsam fir (*Abies balsamea* (L.) Mill.). We found baseline differences in growth. Red maple and yellow birch had the highest growth, sugar maple and red spruce had intermediate growth, and balsam fir had the lowest growth. While some year-to-year declines were associated with specific stress events, protracted patterns such as recent increases in red spruce and red maple growth were correlated with increased temperature and cooling degree days (heat index). For most species and elevations, there was a positive association between temperature and growth but a negative association with growth in the following year. Based on our comparisons, for some species, growth at Mt. Mansfield aligns with regional trends and suggests that patterns assessed here may be indicative of the broader region.

Key words: red spruce, sugar maple, yellow birch, red maple, balsam fir.

Résumé : Dans le nord-est des États-Unis, le dépérissement des arbres associé à l'appauvrissement des sols en calcium causé par les dépôts acides a été documenté, notamment dans le cas de l'épinette rouge (*Picea rubens* Sarg.) et de l'érable à sucre (*Acer saccharum* Marsh.). Il y a des indications contradictoires au sujet des espèces d'arbre coexistantes à savoir si elles ont profité de ce dépérissement ou subi des réductions similaires de croissance, et de quelle façon leur croissance a fluctué en fonction des variables environnementales. Nous avons étudié cinq espèces le long de trois transects altitudinaux sur le mont Mansfield au Vermont : l'érable à sucre, l'épinette rouge, l'érable rouge (*A. rubrum* L.), le bouleau jaune (*Betula alleghaniensis* Britton) et le sapin baumier (*Abies balsamea* (L.) Mill.). Nous avons observé des différences de base dans la croissance. L'érable rouge et le bouleau jaune avaient la plus forte croissance, l'érable à sucre et l'épinette rouge avaient une croissance intermédiaire et le sapin baumier avait la plus faible croissance. Tandis que d'année en année des dépérissements ont été associés à des événements stressant spécifiques, des tendances prolongées, telles que l'augmentation récente de la croissance de l'épinette rouge et de l'érable à sucre, étaient corrélées avec l'augmentation de la température et les degrés-jours de refroidissement (indice de chaleur). Dans le cas de la plupart des espèces et des altitudes, il y avait une relation positive entre la température et la croissance, mais une relation négative avec la croissance de l'année suivante. Sur la base de nos comparaisons, dans le cas de certaines espèces la croissance au mont Mansfield s'harmonise avec les tendances régionales et indique que les comportements évalués ici sont possiblement représentatifs de l'ensemble de la région. [Traduit par la Rédaction]

Mots-clés : épinette rouge, érable à sucre, bouleau jaune, érable rouge, sapin baumier.

Introduction

Regional forests in the northeastern United States (US) reflect temporally and spatially complex land use change in the 19th and 20th centuries that included deforestation, agricultural expansion, and subsequent reforestation (Whitney 1994). Resulting second-growth forests were then subjected to novel anthropogenic stress in the 20th century, notably acid deposition induced nutrient perturbations that altered forest health and productivity (DeHayes et al. 1999; Greaver et al. 2012). In particular, acidic deposition and resulting calcium (Ca) depletion have been associ-ated with health and productivity declines for red spruce (*Picea rubens* Sarg.) (DeHayes et al. 1999) and sugar maple (*Acer saccharum* Marsh.) (Schaberg et al. 2006), two dominant and economically important tree species in the northeastern US. Added to the stress of pollutants and decades of soil cation depletion, anthropogenic emissions of carbon dioxide (CO_2) and other greenhouse gases have induced changes in the global climate. Greenhouse gas accumulations have led to an increase in the annual mean temperatures in the northeastern US of 0.09 °C·decade^{-1} (1895–2011), resulting in a lengthening of the freeze-free period and functional growing season (Kunkel et al. 2013). While precipitation has not

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significantly changed for winter, spring, or summer, fall and annual precipitation totals have increased 0.61 and 0.99 cm·decade⁻¹, respectively (Kunkel et al. 2013). Continued changes in temperature and precipitation, alone and in combination with other stressors, could push trees beyond the environmental thresholds to which they are adapted and result in reduced competitive capacity, growth, and survival for some species compared with others.

Whereas the declines of several tree species associated with acid deposition are well documented in the region, research suggests that some of these chronically stressed species are experiencing contemporary growth increases (Kosiba et al. 2013) and possible range expansion (Beckage et al. 2008; Foster and D'Amato 2015). Both deviations are hypothesized to be associated with changes in environmental factors such as elevated atmospheric CO_2 concentrations, fluctuating atmospheric pollution, and rising temperature. Elevated CO_2 has been proposed to cause a fertilization effect in some trees (Salzer et al. 2009; Soulé and Knapp 2006), but other findings have not supported this (Bader et al. 2013; Girardin et al. 2016; Körner et al. 2005). While acid deposition initially caused declines in some tree species, the enforcement of the Clean Air Act and subsequent amendments has reduced sulfur (S) and, less dramatically, nitrogen (N) deposition (Burns et al. 2011). Removal of this source of damage could allow for a recovery for chronically stressed species, and further, N deposition can promote growth, particularly in N-limited ecosystems (Aber et al. 1998). Rising temperatures could also extend the functional growing season, especially for temperate conifers that retain foliage year-round (Kosiba et al. 2013).

While anthropogenic stress continues to mount within northeastern forests, there is limited evidence of clear trends in forest response; yet, large alterations in tree growth rates could have profound effects on the ecology of these forests, including changes to carbon (C) pools, biogeochemical and hydrological cycles, and species composition. These fluctuations could alter important ecosystem services, including ones with direct economic impacts such as wood products and recreation.

Here, we present growth patterns and trends determined using xylem annual increment measurements for five tree species that characterize the northern hardwood and montane spruce–fir forests: sugar maple, red spruce, red maple (Acer rubrum L.), yellow birch (Betula alleghaniensis Britton), and balsam fir (Abies balsamea (L.) Mill.) growing along elevational transects on Vermont's tallest mountain, Mt. Mansfield. We hypothesized that trees would have different growth rates dependent on species, elevation, and year, with some species displaying muted growth in recent decades. We expected that sugar maple, a species that has experienced geographically broad decline since the 1980s (Horsley et al. 2002), and yellow birch, a species with limited reports of decline (van Doorn et al. 2011), would have reduced recent growth. Conversely, we predicted that red spruce at Mt. Mansfield would show recent increases in growth synchronous with a regional growth pattern of unknown cause (Kosiba et al. 2013). We expected that sympatric balsam fir may have experienced competitive reductions in growth concurrent with increases in red spruce growth. Although red maple stocking and growth in the understory has increased regionally (Abrams 1998), growth trends for dominant and co-dominant red maple are unresolved.

By associating the nature and timing of observed growth relative with local weather and pollution data, we assessed how putative environmental drivers may have influenced species growth and productivity over time. Specifically, we anticipated that deposition of S and N would be negatively associated with red spruce and sugar maple growth, particularly in the 1970s–1990s when deposition was the greatest. We hypothesized that atmospheric CO_2 concentration, summer temperature, and growing season length would be positively associated with growth and that temperature relationships would strengthen with increasing elevation. We expected that increased fall and spring temperatures would be beneficial to evergreen conifers, as they can photosynthesize outside the traditional growing season when sympatric deciduous trees are leafless. We also predicted that metrics of precipitation would have a variable association with tree growth at Mt. Mansfield considering that these trees persisted through severe droughts in the 1930s and 1960s (Dupigny-Giroux 2002), as well as a current pluvial (Pederson et al. 2013).

Methods

Site description

Mt. Mansfield State Forest, part of the northern Appalachian mountain chain, located in north-central Vermont (Underhill, Vermont, USA; 44.5439°N, 72.8143°W), is a 18 000 ha parcel comprised of multiple forest types across an elevational range of approximately 1000 m, with a summit at 1339 m. A northern hardwood forest, dominated by sugar maple, red maple, American beech (Fagus grandifolia Ehrh.), and yellow birch, extends to ~800 m, where it merges in a transition zone with a montane spruce–fir forest, primarily composed of balsam fir and red spruce. Red spruce, a temperate conifer, is frequently found intermixed in the northern hardwood ecotone. The dynamics of the forests are controlled by localized wind events and individual-tree mortality; however, historical timber harvest occurred sporadically in the early 20th century through parts of the Mt. Mansfield State Forest (Cogbill 1996). Soils are primarily stony podzols with considerable areas of rock outcrops, particularly approaching the summit (Soil Survey Staff 2015).

The climate of Mt. Mansfield State Forest is continental, encompassing a large temperature range (Supplementary Fig. S1[1]) and is affected by its proximal location to Lake Champlain, a 126 910 ha lake 24 km west of the study site, which moderates temperature and increases snowfall amounts. The annual mean temperature is 4.2 °C, with an average of 154.6 cm of precipitation deposited uniformly throughout the year (Supplementary Fig. S1[1]) (PRISM Climate Group 2004). January is the coldest month and July is the warmest (–10.5 °C and 17.6 °C average temperature 1925–2012 for study location, respectively) (PRISM Climate Group 2004). Continuous snow cover is the winter norm, persisting over 5 months at higher elevations. Humidity and water availability increase with elevation.
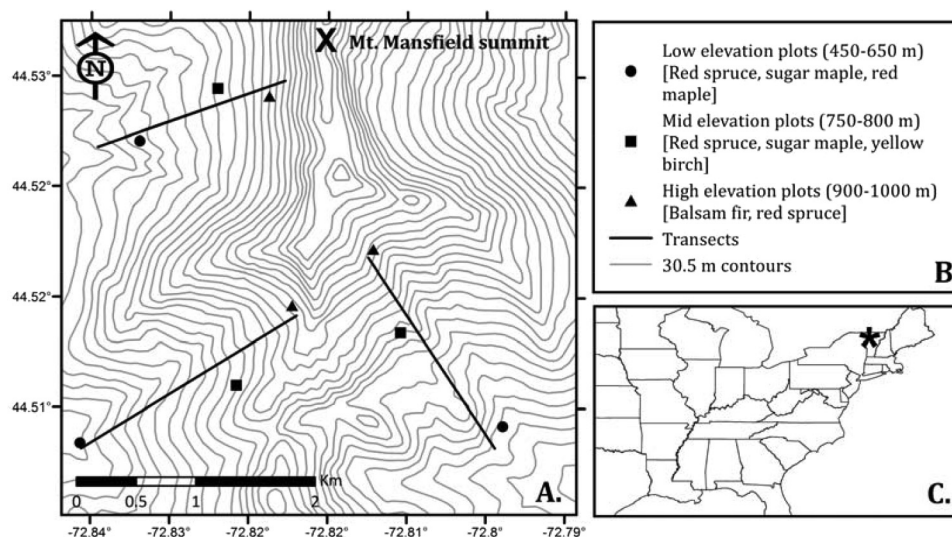
Plot selection

Elevational transects were set up in three of the four watersheds on Mt. Mansfield (Brown's River, Stevensville Brook, and Ranch Brook Watersheds). No transect was established in the fourth watershed because this area has experienced anthropogenic disturbance associated with a commercial ski area. Along each transect, three plots were selected, one within each of the following elevational zones: low (450–650 m a.s.l.), mid (750–850 m), and high (900–1000 m) (n plots = 9; Fig. 1), which align with northern hardwoods, transition, and montane spruce–fir ecotones, respectively. No obvious stand mortality or substantial recent disturbance was evident in any of the plots.

Plots contained 10–14 dominant or co-dominant trees of each of the target tree species equally distributed around plot center to avoid differing competition pressures among trees. Trees with obvious bole or crown damage or those growing in anomalous conditions were not selected. We sampled red maple, sugar maple, and red spruce at low elevation; sugar maple, yellow birch, and red spruce at mid elevation; and red spruce and balsam fir at

Fig. 1. Map of plot locations in Mt. Mansfield State Forest, Vermont, USA, showing (A) three watershed transects, each with three plots located within low-, mid-, and high-elevational zones, (B) species sampled per elevational band, and (C) study site location within the region.

high elevation (Fig. 1). Due to differential species densities across the landscape and different numbers of species sampled per plot, plots were of variable radius (approx. 20–35 m).

We selected species if they were the dominant components of the montane spruce–fir (red spruce and balsam fir) or northern hardwood (sugar maple and yellow birch) forests or if the species has experienced increased dominance in this latter forest type (red maple; Abrams 1998). American beech, a dominant component of the northern hardwood forest, was not assessed because its growth dynamics have been altered following widespread damage from the beech bark disease complex (Gavin and Peart 1993).

Dendrochronology

We increment-cored selected trees (n = 256) following standard dendrochronological techniques (Stokes and Smiley 1968) in the fall of 2012. We collected two 5 mm increment cores per tree at stem diameter at breast height (DBH, 1.37 m above ground level) at 180° and perpendicular to the slope. Cores were air-dried, sanded with progressively finer grit sandpaper (ranging from 100 to 1500 grit depending on species), and visually crossdated using the list method (Yamaguchi 1991). We microscopically measured rings to 0.001 mm resolution using a Velmex sliding stage unit with MeasureJ2X software (VoorTech Consulting, Holderness, New Hampshire) and used the computer program COFECHA to detect and correct for potential crossdating errors in ring series (Holmes 1983). 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)). For descriptive purposes, tree age (at breast height) was calculated using the maximum number of rings per tree if pith was evident or was estimated per core using a pith indicator (Speer 2010) if pith was not reached. For all trees, we were able to estimate age from at least one core.

For the climate analyses, we detrended, standardized, and prewhitened all raw ring width series and computed biweight robust mean chronologies per species per elevation. Descriptive statistics (sample sizes, R bar, expressed population signal (EPS), and signal-to-noise ratio (SNR)) of resulting chronologies were calculated using a running 30-year window with 15-year overlap using Spearman correlation coefficients (Supplementary Table S1[1]) and used to select the best detrending and standardization technique. For all series chronologies, a 67%n cubic smoothing spline (CSS) (dplR package in R), using a frequency response cutoff of 0.5, was used. If this spline was a poor fit, a more conservative horizontal line

was fit to the data. Traditionally, chronologies are truncated at the year when the EPS value falls below 0.85 (Speer 2010), but this would preclude the use of a portion of both the red maple and sugar maple chronologies at low elevations due to their young age and comparatively small sample size. Because results here were used solely to investigate growth–climate and growth–deposition relationships rather than for climatic reconstructions, we reduced the threshold to 0.80, allowing for the use of a common period spanning from 1925 to 2012. However, lower EPS values indicate that these trees have a weaker stand-wide signal and may be more influenced by microsite factors, which could mask a cohesive stand-wide signal. Summary statistics and data on the nine plots and resulting chronologies can be found summarized by species and elevational zone in Supplementary Table S2[1]. Comparisons of growth among species and elevations were done with the Kruskal–Wallis rank sums test followed by the Wilcoxon method for pairwise comparisons, as data did not meet the assumptions of equal variance ($P \leq 0.05$).

We also averaged raw ring widths by tree and converted measurements into basal area increment (BAI, cm²·year⁻¹) assuming a circular outline of stem cross sections (Cook and Kairiukstis 1990) and accounting for bark thickness. BAI is considered a more meaningful indicator of tree growth from a physiological standpoint because it provides an indication of annual stemwood production while accounting for the effects of stem geometry on radial growth associated with tree maturation (Hornbeck and Smith 1985; LeBlanc 1992; West 1980). We then computed biweight robust mean BAI chronologies per species per elevation using the dplR package (Bunn et al. 2015) for R (version 3.1.1; R Core Team 2015) to moderate the effect of large BAI values and (or) outliers on the mean chronology.

Growth associated with climate and deposition

Climate data (maximum and minimum monthly temperature (T_{max} and T_{min}, respectively) and total monthly precipitation (P)) from 1925 to 2012 were obtained from the PRISM Climate Group (PRISM Climate Group 2004). To reduce the number of variables assessed and limit the occurrence of type II errors, we computed seasonal mean (T_{mean}), maximum, and minimum temperatures (Winter, previous December–February; Spring, March–May; Summer, June–August; Fall, September–November), annual water year (previous (p) October to current September) mean temperature, and seasonal and water year precipitation totals. Using monthly data, we also calculated the average temperature for an extended

growing season (May–August and June–September) (Supplementary Fig. S1[1]).

Pollutant S and N deposition data by water year were obtained from the Hubbard Brook Experimental Forest (HBEF; Watershed 1, Thorton, New Hampshire, USA) spanning 1965–2010 (Likens 2010) (Supplementary Fig. S1[1]). As this dataset covers more years than the one from Mt. Mansfield (1984–2012) (National Atmospheric Deposition Program 2014) and the datasets were highly correlated ($R = 0.94$, $P < 0.0001$), we combined them by adjusting HBEF data via regression analysis and then added this to the Mt. Mansfield dataset for continuous coverage from 1965 to 2012. We gathered data of annual atmospheric CO_2 concentration from the Mauna Loa Observatory, Hawaii, USA (NOAA Earth System Research Laboratory Global Monitoring Division 2013), and from Law Dome, Antarctica ice core data (Etheridge 2010); combined for a CO_2 dataset spanning 1925–2012. We also collected the following data: Vermont Palmer Drought Severity Index (PDSI) (National Drought Mitigation Center 2014); three measures of degree days (growing degree days (GDD, measured as cumulative degrees >5 °C (41 °F)), cooling degree days (CDD, >18.3 °C (65 °F)), and heating degree days (HDD, <18.3 °C (65 °F))) for Burlington International Airport, Vermont (NOAA National Weather Service 2014); and monthly Standardized Precipitation–Evapotranspiration Index (SPEI, 1-month) for Vermont, a multiscalar drought and temperature index that includes the effects of evapotranspiration (National Drought Mitigation Center 2012). These datasets were chosen based on proximity or length of record; these datasets covered 1945–2012 (Supplementary Fig. S1[1]).

Growth relationships with climate, deposition, and other data were assessed using "treeclim" (Zang and Biondi 2015) for R, which uses time-dependent bootstrapped resampling (1000 iterations) to test for linear correlations between the residual ring width data and each subvector of the climate matrix (Zang and Biondi 2015). To investigate the dominant drivers of tree growth, we first examined stationary correlations over the common period (or a limited subset for climate and deposition datasets spanning fewer years), including previous year's climate and deposition on current year's growth. Second, to assess the temporal stability of climate–growth relationships, we used the significant variables from the first analysis to evaluate relationships with growth per temporal quartile. Third, we used principal component analysis to examine common modes of growth among species per elevation. Using the first principle component (PC) per elevation, we again examined stationary correlations with our climate and deposition variables. For all analyses, Spearman correlation coefficients were computed with a 99% confidence interval (CI) to reduce the number of input variables, type II errors, and covariation among variables.

Lastly, we used the significant climate and pollution deposition variables from the first analysis to model growth per species and elevation. All variables were first standardized ($\mu = 0$, $\sigma = 1$). If multicollinearity was evident among variables, we used forward stepwise linear regression (using AIC criteria) to reduce selected variables. For all species and elevation pairs, we then created linear models to best explain growth; nonsignificant variables were removed and the model was reassessed. Using the residuals of these models, we then regressed CO_2 data to examine if there was a detectable CO_2 effect after accounting for the dominant climate effects (Girardin et al. 2016).

Comparisons with other chronologies and datasets

We used other crossdated (±0 years) tree ring chronologies collected by the authors or affiliates (Engel et al. 2016; Hansen 2015; Weverka 2012) to compare growth trends on Mt. Mansfield with those of other locations in the region using Pearson product–moment correlation. All chronologies were collected following similar methods described above and converted into BAI. Due to age limits of the chronologies from the HBEF, we constrained

analyses to 1950–2012 for sugar maple and yellow birch (Hansen 2015).

Results

Absolute growth

We found significant and consistent growth differences among the species ($P < 0.001$) (Fig. 2A). Yellow birch and red maple had the largest mean growth (mean BAI ± SD, 15.2 ± 5.1 and 13.0 ± 4.3 cm², respectively). Sugar maple and red spruce were intermediate in growth (7.1 ± 2.0 and 7.7 ± 2.9 cm², respectively), and balsam fir had the lowest growth (4.7 ± 2.4 cm²). These patterns were fairly stable over the quartiles of the chronology, excluding the first quartile (1925–1946) and the most recent growth (2002–2012).

Growth was consistently higher at low and mid elevations compared with high elevation (Fig. 2B) ($P < 0.001$). For the chronology overall and for the central two quartiles (1947–1968, 1969–1990), growth was greater at mid elevations than at low elevation. For all three elevations, overall growth increases in the most recent decade were driven by increases in two species: red spruce and red maple.

For the two species sampled at multiple elevations (sugar maple and red spruce), species-specific growth across elevations showed differing patterns (Fig. 3). Sugar maple at low elevation had significantly higher mean growth than at mid elevation (8.1 ± 2.6 and 6.5 ± 1.7 cm², respectively; $P < 0.01$), juxtaposing the general patterns that mid elevation plots had higher mean BAI overall. For both elevations, sugar maple maximum growth was only slightly higher than the mean and occurred in the third quartile: 1985–1995 for low-elevation and 1970–1990 for mid-elevation trees. Following this peak, both chronologies exhibited slight declines in growth. Mid-elevation red spruce had the highest average growth (13.0 ± 4.3 cm²), with low elevation intermediate (7.8 ± 3.1 cm²), and high elevation the lowest (4.1 ± 3.2 cm²) (Fig. 3) ($P < 0.01$). For red spruce at all elevations, maximum growth occurred in 2012 (year of sampling) and was considerably higher than overall chronology means. At both mid and high elevations, four out of five years of maximum red spruce growth occurred in the years immediately prior to sampling (2009–2012).

Growth trends

Species-to-species comparisons per elevation (Fig. 3) reveal that peak growth varied, but for all species, the highest growth years were in the second half of the chronology (e.g., 1960s to 2012). At low elevation, both red spruce and red maple displayed recent increases in growth, while sugar maple did not. For all three species at low elevation, peak growth roughly coincided; although for both red maple and red spruce, maximum growth persisted longer and was more recent than for sugar maple. At mid elevation, highest growth for yellow birch and sugar maple corresponded (1960s–1980s), yet red spruce peak growth occurred when these neighboring species were showing decreases. At high elevation, balsam fir experienced maximum growth at the end of the 1980s through the early 2000s.

The recent growth surge of red spruce was not seen in the other species at mid elevation. While this increase was most pronounced for low- and mid-elevation red spruce, red spruce growing at high elevation, where growth over the length of the chronology was more stable and constrained compared with lower elevation red spruce, also exhibit this upward trend. At all elevations, red spruce exhibited periods of depressed growth beginning in the mid-20th century that align with suspected or known winter injury events (Johnson et al. 1986; Lazarus et al. 2004).

Climate and deposition relationships with growth

Examining climate–growth relationships using the principal components (PCs) derived from chronologies per elevation, we saw that overall, all three elevations display a positive correlation

Fig. 2. Bi-weight robust mean basal area increment (BAI, cm^2 ± SD, shown with grey bars) by (A) species and (B) elevation from 1925–2012. A nonparametric Kruskal–Wallis test, followed by Wilcoxon each pair test, using species, elevation, and year as factors was significant for the three factors ($P < 0.001$). Different letters following species and elevation categories denote significant differences overall ($P < 0.001$). The model was also significant for each of the four 21-year quartiles (1925–1946, 1947–1986, 1969–1990, 1991–2012; separated by vertical grey dashed lines; $P < 0.001$) for species and elevation, but year was only significant for the period 1925–1946. BF, balsam fir; RM, red maple; RS, red spruce; SM, sugar maple; YB, yellow birch; L, low elevation (450–650 m a.s.l.); M, mid elevation (750–800 m); and H, high elevation (900–1000 m)). Bonferonni adjusted P values were used.
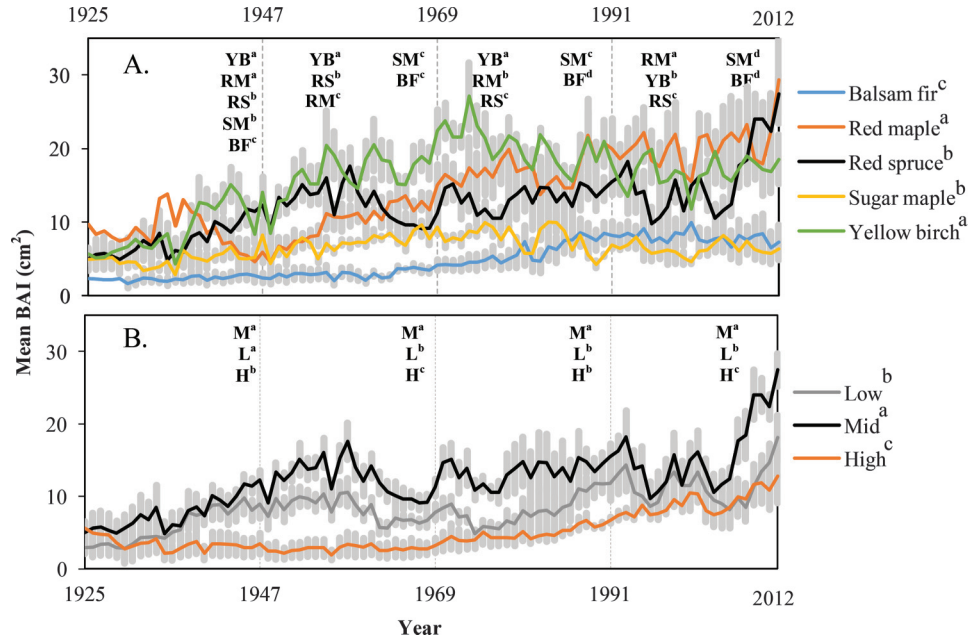
between growth and growing season temperature ($P < 0.01$; Table 1). At low elevation, Summer T_{mean} was best associated with growth ($\rho = 0.38$), along with NH_4^+ deposition ($\rho = 0.35$). Both mid and high elevations showed positive correlations with CDD and growing season temperatures (e.g., Spring and Summer T_{mean}). However, non-growing-season temperatures and PDSI were important to high-elevation trees only. A model of growth at both mid and high elevations identified CDD as the best predictor ($R^2_{adj} = 0.13$, $P = 0.001$, and $R^2_{adj} = 0.10$, $P = 0.04$, respectively). At low elevation, the growth model included a positive effect of May–August T_{mean} ($R^2_{adj} = 0.08$, $P = 0.005$). Atmospheric CO_2 concentration was not significantly associated with growth for any of the species or elevations using either growth, PCs by elevation, or residuals (not shown).

At high elevation, balsam fir growth was positively correlated with temperature ($P < 0.01$; Table 2). The strongest positive correlations occurred with previous year's (p) Fall T_{min} ($\rho = 0.38$) and Spring T_{min} ($\rho = 0.24$), while there was a negative association with pCDD ($\rho = -0.37$) and pGDD ($\rho = -0.31$) (Table 2). Although significant overall ($P < 0.01$), the strength of the relationships between balsam fir growth and other variables declined in the middle of the chronology (1969–1990). The best model to predict balsam fir growth ($R^2_{adj} = 0.19$, $P = 0.0008$) included a negative effect of pCDD ($R^2_{adj} = 0.13$, $P = 0.002$) and a positive effect of Spring T_{min} ($R^2_{adj} = 0.05$, $P = 0.04$).

Red spruce exhibited the strongest positive relationships ($P < 0.01$) with temperature (CDD, GDD, and water year T_{mean}), including a strong correlation with non-growing-season temperature (Table 2). Indeed, water year T_{mean} was positively associated with red spruce growth at all elevations and, while not always significant, displayed a consistently positive correlation with growth across quartiles. As with the other species, pCDD was strongly, negatively correlated to red spruce growth, and this pattern persisted through time ($P < 0.01$). At both mid and high elevations, there was a positive association between growth and
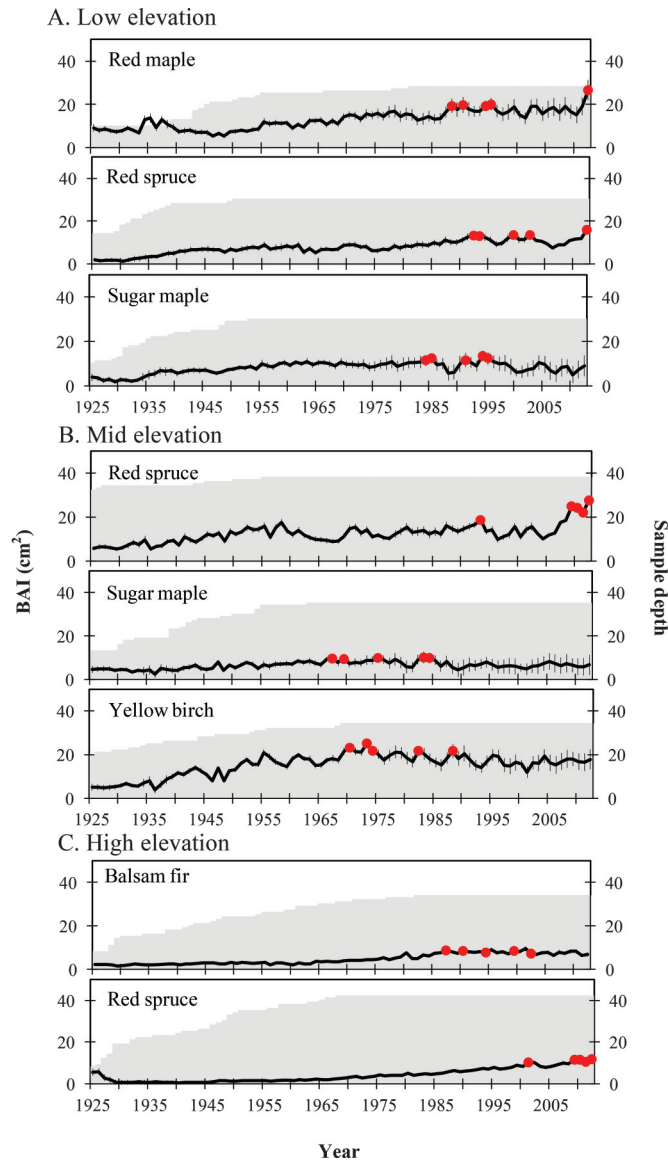
pWinter T_{max} ($\rho = 0.27$ and 0.23, respectively). This relationship was negative in the third quartile, 1969–1990. Interestingly, pNO$_3$ deposition was negatively associated with growth of red spruce at low elevation ($P < 0.01$, $\rho = -0.37$), which strengthened through the quartiles of the chronology.

For red spruce at low elevation, we found that the negative effects of both HDD ($R^2_{adj} = 0.11$, $P < 0.0001$) and pCDD ($R^2_{adj} = 0.15$, $P < 0.0001$) were the best predictors of growth in a linear model ($R^2_{adj} = 0.40$, $P > 0.0001$). At mid elevation, the best model ($R^2_{adj} = 0.31$, $P < 0.0001$) included a positive effect of water year T_{mean} ($R^2_{adj} = 0.13$, $P = 0.0006$) and, as at low elevation, a negative effect of pCDD ($R^2_{adj} = 0.12$, $P = 0.0002$). At high elevation, the best model included a negative effect of both pCDD ($R^2_{adj} = 0.09$, $P = 0.0001$) and HDD ($R^2_{adj} = 0.11$, $P = 0.018$) and a positive effect of GDD ($R^2_{adj} = 0.19$, $P = 0.017$) (overall model $R^2_{adj} = 0.35$, $P < 0.0001$).

Measures of degree days and temperature were also important for red maple growth at low elevation ($P < 0.01$) (Table 2). Growing season temperature (i.e., Summer T_{mean}, June–September T_{mean}, and CDD) was positively correlated with red maple growth ($P < 0.01$, $\rho = 0.30$, 0.26, and 0.39, respectively), while preceding year's heat accumulation (pCDD) was negatively associated ($\rho = -0.34$). For red maple, the best growth model ($R^2_{adj} = 0.20$, $P = 0.0004$) included a negative effect of pCDD ($R^2_{adj} = 0.11$, $P = 0.002$) and a positive effect of Summer T_{mean} ($R^2_{adj} = 0.08$, $P = 0.006$).

At low elevation, sugar maple growth was not correlated ($P > 0.01$) with the selected variables (Table 2); therefore, we were unable to create a model of growth. For sugar maple at mid elevation, Summer T_{mean} was positively associated with growth ($P < 0.01$, $\rho = 0.26$). However, this relationship was not consistent through the quartiles. As in many of the other species in this study, growth for these trees also exhibited a negative correlation ($P < 0.01$) with pSummer T_{mean} ($\rho = -0.25$) and pSummer T_{max} ($\rho = -0.27$), as well as with pCDD ($\rho = -0.38$). To model growth, we were limited by the number and high collinearity of input variables. Both pSummer T_{mean} and pSummer T_{max} explained a similar

Fig. 3. Mean (±SD) basal area increment (BAI, cm²; solid black line) chronologies per species and elevational zone: (A) low 450–650, (B) mid 750–800, and (C) high 900–1000 m a.s.l. elevation from 1925 to 2012 in Mt. Mansfield State Forest, Vermont. Number of trees contributing to the mean is shown with grey bars. Red circles designate the five highest growth years per chronology.

Table 1. Significant correlations from stationary climate–growth assessments for all species combined per elevation for trees from Mt. Mansfield, Vermont, as evaluated using principal component analysis (1925–2012).

Elevation[a]	Positive		Negative	
	Variable[b,c]	Correlation coefficient	Variable[b]	Correlation coefficient
High	Water year T_{mean}	0.34	HDD	−0.38
	pWinter T_{max}	0.25		
	pFall T_{min}	0.40		
	Winter T_{mean}	0.26		
	Spring T_{mean}	0.27		
	CDD	0.37		
	GDD	0.39		
	PDSI	0.36		
Mid	Summer T_{mean}	0.33		
	May–June T_{mean}	0.32		
	June–September T_{mean}	0.36		
	CDD	0.34		
	pFeb SPEI	0.43		
	pDec SPEI	0.38		
Low	pSpring T_{max}	0.25	March SPEI	−0.27
	Summer T_{mean}	0.38		
	May–August T_{mean}	0.28		
	pMar SPEI	0.28		
	NH_4^+	0.35		

Note: Significance based on 99% confidence interval.

[a]Elevations: low, 450–650 m a.s.l.; mid, 750–850 m; and high, 900–1000 m.

[b]Variables: CDD, cooling degree days (cumulative degrees >18.3 °C (65 °F)); Fall, September–November; GDD, growing degree days (cumulative degrees >5 °C (41 °F)); HDD, heating degree days (cumulative days <18.3 °C (65 °F)); max, maximum; min, minimum; p, previous year; PDSI, Vermont Palmer Drought Severity Index; SPEI, Standardized Precipitation–Evapotranspiration Index; Spring, March–May; Summer, June–August; T, temperature; Winter, previous December–February. For more information on variables, see Methods.

[c]Not all variables span the entire chronology (1925–2012, 1945–2012, or 1965–2012). See Methods.

with those species from the HBEF collected in 2012 (Hansen 2015). For sugar maple (*n* trees HBEF = 163; Fig. 4B), the chronologies were significantly correlated ($R = 0.57$, $P < 0.0001$), but for yellow birch (*n* trees HBEF = 170; Fig. 4C), they were not ($R = −0.19$, $P = 0.13$).

Discussion

Patterns of growth

Significant and consistent growth differences among the species highlight their divergent silvics (Burns and Honkala 1990). Yellow birch and red maple, which are intermediate in shade tolerance with moderately high growth potentials (Burns and Honkala 1990), had the greatest mean growth. Sugar maple and red spruce, which are both shade tolerant with the ability to display higher growth when a mature component of the canopy (Burns and Honkala 1990), were intermediate in growth, while balsam fir, highly shade tolerant and with the potential for constrained growth with elevated stocking (Burns and Honkala 1990), displayed the lowest growth. Species-to-species comparisons per elevation reveal that peak growth varied over time, but for all species, the highest growth years occurred in the second half of the chronology.

Lower growth and more muted disparities among the species in the first quartile of the chronology may signify that competition during stand maturation was a strong constraint on growth. Historical anthropogenic land clearing has left a legacy on the forests of Mt. Mansfield evident in the ages of sample trees (Supplementary Table S1[1]). In the absence of a substantial natural disturbance, it is likely that selective logging has resulted in the age divergence among the species and elevations. Cogbill (1996) outlined several

amount of growth variation when fit separately ($R^2_{adj} = 0.06$, $P = 0.01$ for both).

We did not find any negative correlations between yellow birch growth and the variables selected (Table 2). Yellow birch, however, did display positive associations with Summer T_{mean} ($P < 0.01$, $\rho = 0.29$), and these trends were consistent through the quartiles of the chronology. However, when we modeled growth using Summer T_{mean}, only a small amount of growth variation was explained ($R^2_{adj} = 0.07$, $P = 0.008$).

Comparisons with other chronologies

We compared red spruce growth from this study with red spruce from a wide range of plots in Vermont, New Hampshire, and Massachusetts (*n* trees = 452) collected in 2010, 2011, and 2012 (Engel et al. 2016; Kosiba et al. 2013; Weverka 2012). The chronologies were significantly correlated ($R = 0.92$, $P < 0.0001$; Fig. 4A). We also compared sugar maple and yellow birch from this study

Table 2. Correlations from stationary climate–growth assessments from Mt. Mansfield, Vermont, shown by species and elevation for the entire chronology (1925–2012) and by chronology quartile.

Species	Elevation[a]	Variable[b]	Overall 1925–2012[c]	Quartiles 1925–1946	1947–1968	1969–1990	1991–2012
Balsam fir	High	pFall T_{min}	**0.38**	0.29	0.48	0.44	0.30
		Spring T_{min}	**0.24**	0.17	0.59	0.19	0.08
		pCDD	**−0.37**		−0.47	−0.17	**−0.88**
		pGDD	**−0.31**		−0.48	0.03	−0.88
Red maple	Low	CDD	**0.39**		0.24	0.34	**0.65**
		Summer T_{mean}	**0.30**	0.37	0.22	0.31	**0.55**
		Jun–September T_{mean}	**0.26**	0.43	0.28	0.26	0.43
		pCDD	**−0.34**		−0.59	−0.27	−0.17
Red spruce	Low	Water year T_{mean}	**0.43**	**0.44**	**0.52**	0.24	0.48
		pFall T_{min}	**0.32**	0.19	0.41	0.23	**0.53**
		Winter T_{mean}	**0.26**	0.14	0.39	−0.04	0.52
		Spring T_{mean}	**0.36**	0.34	0.37	0.26	0.46
		May–August T_{mean}	**0.28**	0.27	0.29	0.16	0.37
		June–September T_{mean}	**0.43**	0.31	**0.48**	0.01	0.13
		pCDD	**−0.35**		−0.40	−0.31	−0.39
		HDD	**−0.37**		−0.46	−0.05	−0.50
		GDD	**0.38**		0.46	0.21	0.37
		PDSI	**0.36**		0.44	−0.56	0.10
		pNO$_3^-$	**−0.37**		−0.164	−0.17	−0.46
	Mid	Water year T_{mean}	**0.27**	0.35	**0.53**	0.17	0.42
		pWinter T_{max}	**0.27**	0.38	**0.55**	−0.19	0.37
		June–September T_{mean}	**0.26**	0.29	0.49	0.12	0.17
		pCDD	**−0.41**		−0.38	−0.51	−0.40
		GDD	**0.34**		0.44	0.13	0.39
		May SPEI	**−0.30**		−0.15	−0.29	−0.44
	High	Water year T_{mean}	**0.36**	0.28	**0.47**	0.27	0.41
		pWinter T_{max}	**0.23**	0.36	0.46	−0.07	0.24
		pFall T_{min}	**0.32**	0.05	**0.53**	−0.28	0.52
		Winter T_{mean}	**0.26**	0.16	0.22	0.13	0.41
		Summer T_{max}	**0.27**	−0.03	0.31	0.38	0.45
		Fall T_{mean}	**0.23**	0.39	0.28	0.25	0.11
		June–September T_{mean}	**0.31**	0.06	**0.55**	0.48	0.41
		May–August T_{mean}	**0.33**	0.04	0.39	0.46	0.20
		pCDD	**−0.32**		−0.44	−0.29	−0.37
		CDD	**0.42**		0.36	0.43	0.50
		HDD	**−0.34**		**−0.45**	0.07	−0.44
		GDD	**0.45**		0.50	0.30	−0.49
Sugar maple	Low		N/S				
	Mid	pSummer T_{mean}	**−0.25**	−0.12	−0.40	−0.23	−0.22
		pSummer T_{max}	**−0.27**	−0.25	−0.38	−0.28	−0.09
		Summer T_{mean}	**0.26**	0.19	0.45	0.08	0.33
		pCDD	**−0.38**		**−0.55**	−0.29	−0.23
Yellow birch	Mid	Summer T_{mean}	**0.29**	0.37	0.29	0.29	0.29

Note: Coefficients in bold type are significant at 99% CI. N/S, not significant.

[a]Elevations: low, 450–650 m a.s.l.; mid, 750–850 m; and high, 900–1000 m.

[b]Variables: CDD, cooling degree days (cumulative degrees >18.3 °C (65 °F)); Fall, September–November; GDD, growing degree days (cumulative degrees >5 °C (41 °F)); HDD, heating degree days (cumulative days <18.3 °C (65 °F)); max, maximum; min, minimum; p, previous year; PDSI, Vermont Palmer Drought Severity Index; SPEI, Standardized Precipitation–Evapotranspiration Index; Spring, March–May; Summer, June–August; T, temperature; Winter, previous December–February. For more information on variables, see Methods.

[c]Not all variables span the entire chronology (1925–2012, 1945–2012, or 1965–2012). See methods.

logging events in the Stevensville Brook Watershed on the western flank of Mt. Mansfield, and it is suspected that widespread harvesting occurred in the other watersheds as well. Assessment of stand dynamics (data not shown) confirmed that release events were stochastic and not consistent within or among plots.

Some of the year-to-year variations in growth (Fig. 3) can be attributed to known biotic and abiotic stressors. For example, specific low growth years for sugar maple are likely associated with the 1993 infestation of pear thrips (*Taeniothrips inconsequens* (Uzel)) and a late spring frost in 2010 (Hufkens et al. 2012; Vermont Agency of Natural Resources Department of Forest Parks and Recreation 2010). While this late frost event could have affected

sugar maple at low elevation, because no coincident downturn in growth was evident at mid elevation (Fig. 3), we suspect that mid-elevation trees were unaffected due to a later timing of bud break relative to frost exposure. Additionally, a severe ice storm in 1998 that broke the limbs of many hardwood species (Rhoads et al. 2002) was reported for many mid- and high-elevation sites (Vermont Agency of Natural Resources Department of Forest Parks and Recreation 2013). Areas of high ice loading align with our mid-elevation zone and, when followed by a severe drought in 1999, may have caused the growth declines for yellow birch and sugar maple evident in 1999 through 2000 (Fig. 3). Lastly, declines in growth apparent for red spruce at all elevations (Fig. 3) corre-

Fig. 4. Comparisons of mean (±SD) basal area increment (BAI, cm²) for red spruce, sugar maple, and yellow birch from this study on Mt. Mansfield with (A) sugar maple and (B) yellow birch at Hubbard Brook Experimental Forest (HBEF), New Hampshire, and (C) red spruce in the region (34 plots in Vermont, New Hampshire, and Massachusetts). Spearman correlation coefficients (R) and associated P values are shown in each figure. Chronologies at HBEF were limited to 1950–2012.
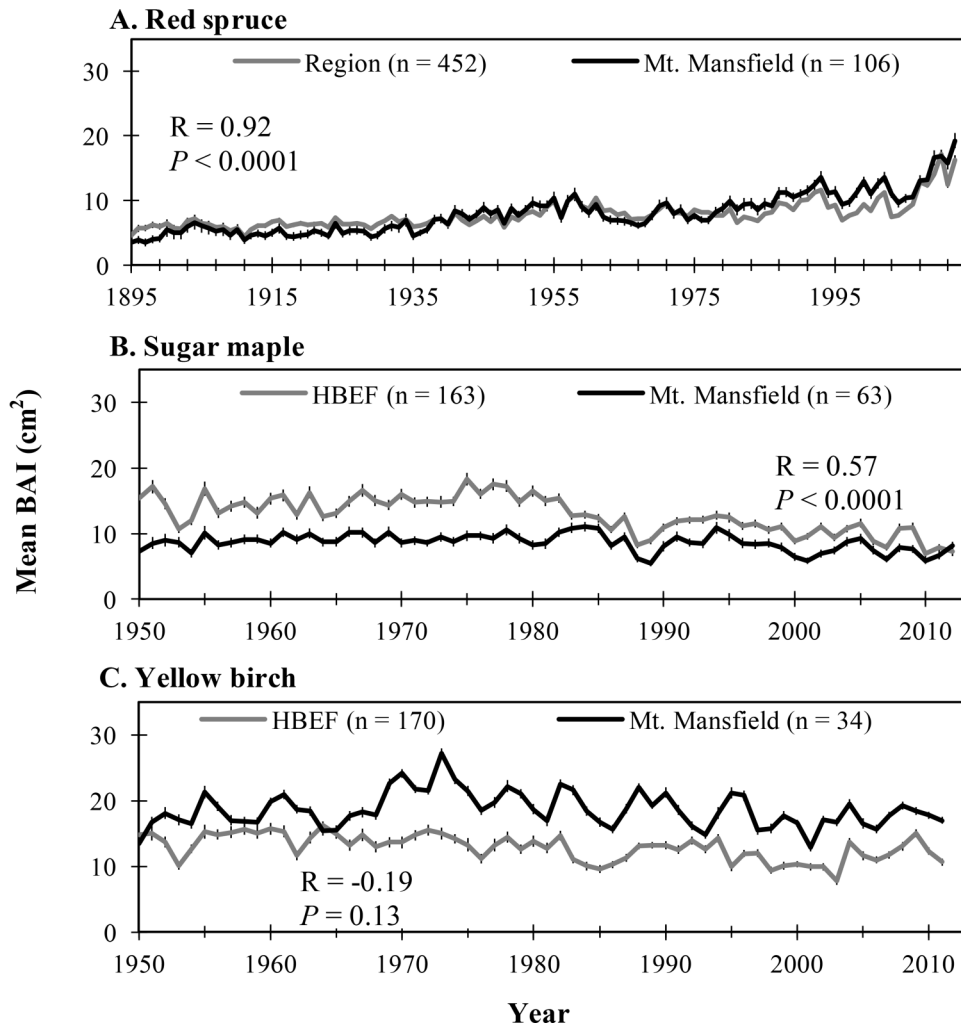
spond with documented winter injury events (Johnson et al. 1986), including in 2003, which was a severe event across the region (Lazarus et al. 2004).

At high elevation, balsam fir experienced maximum growth at the end of the 1980s through the early 2000s (Fig. 3), which parallels the documented decline of red spruce (Lazarus et al. 2004) and suggests that balsam fir was able to capitalize on the resulting foliar losses and growth declines of sympatric red spruce. Balsam fir is not affected by winter injury due to its extreme cold tolerance (DeHayes et al. 2001). Since 2003, a substantial winter injury event has not occurred in the region (Vermont Agency of Natural Resources Department of Forest Parks and Recreation 2013), which may, in part, explain the increase in red spruce growth relative to balsam fir. However, despite some differences over time, at high-elevation plots, both red spruce and balsam fir had relatively low growth due to limitations in growing season length and lower annual temperature.

We detected growth reductions for sugar maple at both low and mid elevations that are temporally consistent with regional declines attributed to acid deposition induced Ca depletion combined with other stress exposures (Schaberg et al. 2006). In this study, growth declines were more dramatic for sugar maple at mid elevation than at low elevation. As acid deposition is more severe with increasing elevation (Johnson and Siccama 1983), mid-elevation sugar maple may have suffered from Ca depletion more extensively and earlier than trees at lower elevation. Indeed, other studies have indicated that sugar maple at mid and high elevations display greater signs of physiological stress from Ca depletion than those at low elevation (Minocha et al. 2010). Although sugar maple growth measurements reported here are low compared with the other sampled species, they are not atypical when compared with other dendrochronological studies in eastern North America (Bishop et al. 2015; Duchesne et al. 2003; Hansen 2015; Long et al. 2009).

Red spruce on Mt. Mansfield have experienced a recent growth increase consistent with other locations (Figs. 2 and 3) (Kosiba et al. 2013). This increase is especially pronounced at mid elevations, which has been previously demonstrated (Kosiba et al. 2013). However, the other species at mid elevations did not display an analogous increase in growth, discounting stand dynamics for this rapid change.

Regardless of species-specific growth, mid-elevation plots displayed significantly higher growth than low- and high-elevations plots. This could signify that mid-elevation sites provide more advantageous conditions for tree growth than either lower or higher elevation (e.g., for red spruce), or it could be confounded by the fact that the fastest growing species for all quartiles (yellow birch) was only sampled at mid elevations.

Red maple also recently exhibited increased growth. However, because this study surveyed a relatively small number of red maple and comparably few studies have examined red maple growth in the region, it is difficult to assess the extent of this growth surge at this time (see Silva et al. 2010; Zhang et al. 2015). Additionally, because red maple was only sampled at low elevation, we do not to know if elevation influences this apparent growth increase. Limited reports on red maple have revealed that its abundance increased dramatically in the 20th century (Siccama 1971), due in part to its purported niche as a "super-generalist" and large ecological amplitude, which permitted competitive growth advantages at a range of site conditions (Abrams 1998).

Relationships with climate and deposition

As expected, growth associations among species and elevations had differing relationships to local climate and deposition. Two general growth associations were evident: (*i*) a positive correlation with higher temperature in the year of growth (particularly for red maple and red spruce and, to a lesser extent, balsam fir, yellow birch, and sugar maple) and (*ii*) a negative correlation with excessive heat (CDD, cumulative temperatures > 18.3 °C) during the previous year (for all species except yellow birch). Positive relationships between temperature and growth imply that low temperature restricted growth. Negative relationships between temperature and growth in the following year suggest a legacy effect of higher temperature, conceivably through limitations of C or other compulsory elements. For example, higher temperature could increase contemporary growth if the tree consumes C for immediate needs such as increased maintenance respiration, growth, or reproductive buds rather than storing C to support growth during the next year (Rennenberg et al. 2006). Similarly, temperature-induced increases in growth could result in the sequestration of other nutrients (e.g., N, Ca) that temporarily become limiting and indirectly suppress growth during the following year (Rennenberg et al. 2006).

Using CDD in growth–climate relationships provides a readily available index of integrated heat exposure that was consistently associated with growth for trees at Mt. Mansfield. Measures of growing season temperatures were important for both mid and low elevations, while water year temperature and pFall T_{min} were important at high elevations. Trees at both high and mid elevations displayed a positive growth correlation with CDD. By quartile, it is clear that climate–growth relationships were not steady through time (Table 2). For some species and variables, associations reversed for one or more quartiles, complicating our ability to predict tree responses to these variables.

Non-growing-season temperature was important for the two conifers in this study. For both balsam fir and red spruce, mild autumn temperatures can delay cold hardening, which allows the foliage to remain photosynthetically active for a prolonged period. Additionally, because red spruce is a temperate conifer that can photosynthesize in fall, winter, and spring, provided that temperatures are moderate (Schaberg and DeHayes 2000), it has been hypothesized that the notable and recent increase in growth could be due to climatic warming that has lengthened the functional growing season for red spruce (Kosiba et al. 2013).

At mid elevations, there was a positive association between red spruce growth and pWinter T_{max}, suggesting that warmer winter temperatures could provide increased growth opportunities for this species. This finding has been reported by others (Cook et al. 1987; McLaughlin et al. 1987). Interestingly, this relationship was negative in the third quartile, 1969–1990, a period of peak acid deposition (Greaver et al. 2012) and documented red spruce decline (Hornbeck et al. 1986; Johnson et al. 1988). When warm winter temperatures cause thaws, red spruce can photosynthesize while sympatric species remain dormant; however, when cold temperatures return, freezing damage can ensue. This process is exacerbated by acid deposition, which reduces the cold tolerance of red spruce foliage (Schaberg and DeHayes 2000).

Red spruce growth at the Mt. Mansfield study plots corresponds well with red spruce growth region-wide, implying that growth trends in this study are not a by-product of local stand dynamics and, further, that climate–growth and deposition–growth relationships presented here may be representative of a region-wide phenomenon. Positive associations with measures of growing season length and temperature (e.g., water year T_{mean}, June–September T_{mean}, GDD, CDD) allude to continued favorable growth conditions and potential range expansion (e.g., Foster and D'Amato 2015) for red spruce into the future. This conclusion contrasts with projected species range maps that depict red spruce range constriction in the future (Iverson et al. 2008). Interestingly, the period of most divergent growth between Mt. Mansfield and regional red spruce was from roughly 1980 through 2008. This period was 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 higher than average growth at Mt. Mansfield relative to the regional chronology may indicate that red spruce on Mt. Mansfield experienced less winter injury than the regional norm. Likewise, the recent synchronous increase in growth evident in the chronologies indicates that this rebound is a regional phenomenon, similar to the ubiquitous decline in growth following the 2003 winter injury event.

In contrast with the other species, sugar maple growth at low elevation was not correlated with the selected variables, suggesting that they may be responding to microsite parameters not considered in this analysis (e.g., nutrient availability, stand dynamics, local soil moisture, etc.). For example, PDSI is a metric for the whole state of Vermont that does not consider site-based soil and hydrological differences that may help explain tree growth. Others have also shown similar weak climate–growth relationships for sugar maple in the region (e.g., Bishop et al. 2015). Sugar maple growth at mid elevations exhibited a negative correlation with pSummer T_{mean} and T_{max}, indicating that elevated summer temperature due to climate change (Kunkel et al. 2013) could limit sugar maple growth further in the future.

Sugar maple at HBEF (Hansen 2015) had higher growth than those at Mt. Mansfield, particularly during the first half of the chronology. After 1982, the chronologies are more analogous. Sugar maple at Mt. Mansfield displayed a subdued decline in growth in the 1980s, but otherwise maintained consistent low growth. It is unclear why sugar maple at HBEF had higher growth than those at Mt. Mansfield for the first part of the chronology, although higher acidic loading in the west of the region (e.g., Ollinger et al. 1993) could have stressed sugar maple trees there first. However, the near-steady growth of sugar maple at Mt. Mansfield since 1950 (Fig. 2) seems inconsistent with the possibility of early stress from acidic inputs. Another possibility is that Mt. Mansfield is a more marginal site for sugar maple growth, so baseline growth there was consistently lower.

Growth of Mt. Mansfield yellow birch did not correspond well with yellow birch growing at HBEF (Hansen 2015). One possible explanation for this could be the lower sample size for yellow birch (*n* = 34 trees) relative to sugar maple (*n* = 63 trees) at Mt. Mansfield, which could reduce the accuracy of yearly growth mean estimates and increase the variation around those means. These results demonstrate the importance of having high replication when looking at region-wide patterns in tree cores.

Surprisingly, annual S and N deposition only related to poor growth for red spruce at low elevation, but not at mid and high elevations where documented declines have been tied to acid deposition (DeHayes 1992; Schaberg et al. 2006). While growth of sugar maple and red spruce, aside from low elevation, did display negative correlations with S deposition, these relationships were not significant. One possible reason for this outcome is the absence of long-term S and N deposition data. Datasets in this region only span from 1965 to 2012, which excludes over a decade of acid deposition inputs. In addition, detrending growth data with a

flexible spline removes high frequency variation and biological trends while preserving decadal and longer trends. Nevertheless, a smoothing spline is one of the best options for reducing the effects of tree competition and age-related growth trends. Lastly, relating growth to annual deposition data may overlook more complex impacts of pollutant loading such as long-term cumulative Ca depletion. For example, research has shown that red spruce growth was related to the historic accumulation of acidic inputs relative to the capacity of the site to buffer these inputs (Engel et al. 2016).

Atmospheric CO_2 concentration trends were not associated with growth (or residuals of growth–climate models after accounting for the effects of climate) for any of the species or elevations. Our findings align with those of others who have shown no significant effect of elevated CO_2 concentration on stem growth (e.g., Bader et al. 2013; Girardin et al. 2016; Körner et al. 2005). While it is currently debated whether elevated CO_2 concentrations will provoke changes in tree growth, there is evidence that CO_2 effects are muted or nonexistent on sites where other environmental factors, including soil fertility (particularly N limitation) (Oren et al. 2001), temperature, and water (Körner et al. 2005), are more limiting to stem growth than C (Körner 2003; Silva and Anand 2013). Based on the strong associations with growth of trees in this study and measures of heat that we reported here, we hypothesize that temperature is more limiting to these trees than C availability.

Conclusions

We presented a comparison of growth trends for five key tree species. While this is a case study, by comparing the chronologies developed at this site with others in the region, we show that at least for red spruce, there is strong alignment to the broader region and propose that patterns evident here may be indicative of the region's forested ecosystems. Comparisons of the chronologies (Fig. 2) highlight that the five species often experienced changes in growth that were either species- or elevation-specific. There was a high degree of year-to-year variability in growth, likely due to local abiotic and biotic factors. For some species, the repeated stress of abiotic and biotic factors in succession may help explain prolonged growth declines.

For most species and elevations, there was a positive association between higher temperatures and growth during that same year, suggesting that contemporary warming has improved the competitive status of many trees. However, there are two noted exceptions to this trend. The first is that excessive heat (CDD cumulative temperatures > 18.3 °C) during the previous year was broadly associated with lower growth in the following year. Further investigation is needed to understand the complex interplay of elevated temperature and net growth in successive years and over time. The second exception is that sugar maple trees at low elevation showed no positive association with increased warming. This may provide field-based evidence of the sensitivity of sugar maple to the warming that has been projected by climate change range models (e.g., Iverson et al. 2008).

Declines of red spruce have also been well documented, but the recent and surprising growth surge had not been investigated. Here we show that it occurred across elevations and watersheds and that perhaps another species, red maple, has had a synchronous increase in growth. Both species show positive correlations with growing season temperatures, including CDD. Indeed, CDD was consistently associated with increased growth for most of the species and elevations overall. This finding highlights the potential value of CDD as an integrated temperature index with relevance to tree growth in a warming world. While CDD was often positively associated with growth, pCDD often had a negative relationship. As CDD increases in the future, its influence on tree growth could be mixed. Results of this analysis suggest that some

tree species may be responding favorably to changing environmental conditions, while others are either declining or appear stable in growth. Though this specific study covered a small spatial scale, it opens avenues for future work 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 among species in the region; yet, this is of interest as the climate changes and the future state of forest health and productivity remains uncertain.

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