



Growth trends and environmental drivers of major tree species of the northern hardwood forest of eastern North America

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Abstract The future health and productivity of tree species in the northern hardwood forest of eastern North America are uncertain considering changes in climate and pollution loading there. To better understand the trajectory of the northern hardwood forest, we studied the growth of three tree species emblematic of it: sugar maple (*Acer saccharum* Marsh), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton), plus a fourth species, red maple (*Acer rubrum* L.), whose abundance has increased in the region. We also analyzed the link between growth and several factors for 690 trees in 45 plots throughout Vermont, USA: tree age and size, site elevation, and climate and acid deposition variables.

Throughout their chronologies (1945–2014), all four species exhibited increasing growth followed by plateaued growth indicative of a maturing forest. For all species, summer moisture was positively correlated with growth, summer temperature was negatively associated with growth, and winter moisture or snow were positively correlated with growth. This last association was expected for sugar maple. However, our data suggest that winter snowpack may be more broadly relevant in sustaining tree growth in a region where snow has historically insulated the soil from freezing that can damage roots and lead to reduced aboveground growth. Measures of pollution deposition were also correlated with growth for all species except American beech—a species with documented tolerance to pollutant inputs. Of the four species studied, red maple had the fewest associations with environmental variables, which suggests that it may be less susceptible to growth reductions as the climate changes.

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Introduction

Recent large-scale studies in North America and Europe show that moisture and drought sensitivity are major drivers of change in tree species abundance (Mette et al. 2013; Bose et al. 2017; Fei et al. 2017) and growth (Martin-Benito and Pederson 2015; Bosela et al 2018; D’Orangeville et al. 2018). The northeastern United States (US) and adjacent Canada have experienced an unprecedented amount of precipitation over the last several decades (e.g., Pederson et al. 2013), a pattern that is expected to continue or even increase as climate change progresses (Janowiak et al. 2018). However, while precipitation rates have risen, this increase has not been distributed equally across all seasons (Kunkel

et al. 2013). Growing season moisture has been shown to be a driving factor of growth for numerous tree species (D'Orangeville et al. 2018). But for species specifically adapted to the northern hardwood forests of northeastern North America, a changing hydrological regime during the non-growing season may have a substantial influence on growth as well. For example, tree species of the northern hardwood forest are adapted to winters with consistent periods of snowpack. But in recent decades, winter precipitation has increasingly fallen as rain, reducing winter snowpacks, which could detrimentally affect tree species' health and productivity (Reinmann et al. 2019). In addition to a shift in seasonal moisture patterns, increases in temperature have not occurred uniformly across all seasons in the Northeast. Winter temperatures—in particular, minimum winter temperatures—have exhibited the greatest increases amongst seasons (Janowiak et al. 2018). Understanding how these nuanced seasonal changes in moisture and temperature are affecting tree communities is crucial to managing the iconic northeastern forests (Swanston et al. 2018) for the current and future ecological, economic, and recreational services that they provide.

The three major species of the northern hardwood forest are sugar maple (*Acer saccharum* Marsh), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton). Despite extensive research on the decline of sugar maple in the northeastern US and eastern Canada (Horsley et al. 2002), few recent studies exist that link climate factors to the growth of these species in Vermont (VT), which is in the heart of the northern hardwood forest. For a state that is 76% forested (Morin 2018), VT provides an ideal testing ground for unlocking the key drivers of past and present growth for these distinctive species. In addition to traditionally abundant species in the northern hardwood forest, questions about how shifting climate patterns might affect the relative importance of other species must be considered, since different tree species can have varying effects on ecosystems (Loreau et al. 2001). One species that has been increasing its abundance in the Northeast is red maple (*Acer rubrum* L.) (Fei and Steiner 2007; Pontius et al. 2016). Few studies have been done in the Northeast linking climate factors to the growth of this prolific species, but empirical evidence of how tree species are faring with a changing climate is vital to forest management and resiliency plans.

One key to understanding and managing for the future trajectory of all four tree species is knowing how they have responded to past environmental factors. Only by discerning how trees have responded in the past can we understand how tree response may be shifting as a result of changing climate regimes and decreased pollution (Kosiba et al. 2018). Sugar maple health has been well documented as being negatively affected by inputs of acid deposition (e.g., Schaberg et al. 2010; Halman et al. 2013) and soil cation depletion (Hallett

et al. 2006). Whether pollution deposition has affected other species has been surprisingly under explored. If certain species show little change in these associations to environmental cues over time, that may reflect their ability to thrive regardless of a changing climate. Tree-ring data can provide a high-resolution retrospective view of climate-growth relationships for regional tree communities.

To evaluate potential associations with both climate and pollutant deposition factors among all four species, we measured tree rings for 690 dominant and co-dominant trees at 45 plots at varying elevations in VT, and statistically compared growth to tree and stand characteristics and regional climate and pollutant deposition data. For all four species—sugar maple, American beech, yellow birch, and red maple, our specific objectives were to: (1) characterize growth patterns of the last several decades; (2) analyze the growth responses of each species to climate; (3) investigate potential growth responses to pollutant deposition; and, (4) look for differences in climate- and deposition-growth associations due to elevation or over time. We hypothesized that:

H₁ Moisture availability would be an important driver of growth for species emblematic of the northern hardwood forest (sugar maple, yellow birch and American beech) but would be less so for red maple, which is considered to be a generalist species that is competitive across a range of environments (Burns and Honkala 1990).

H₂ Temperature would be of lesser importance in influencing growth because our study sites are not near the southern or northern range limits of any of the species studied.

H₃ Pollution would be negatively associated with growth, but that its influence would be species-dependent (e.g., greater for sensitive species like sugar maple than for American beech, which is thought to be less sensitive to the impacts of acid precipitation (e.g., Halman et al. 2014)).

H₄ Elevation would also have limited influence on growth because the northern hardwood stands sampled straddled a limited elevational gradient.

Materials and methods

Study sites

The study area is located in VT, ranging from 43.0547° N to 44.9324° N latitude and 73.2541° W to 71.7164° W longitude (Fig. 1). Average temperature (1945–2014) is warmest in July (25.4 °C) and coldest in January (−14.7 °C); mean annual precipitation is 1110 mm, with 47% of precipitation falling from May through September (Fig. 2;

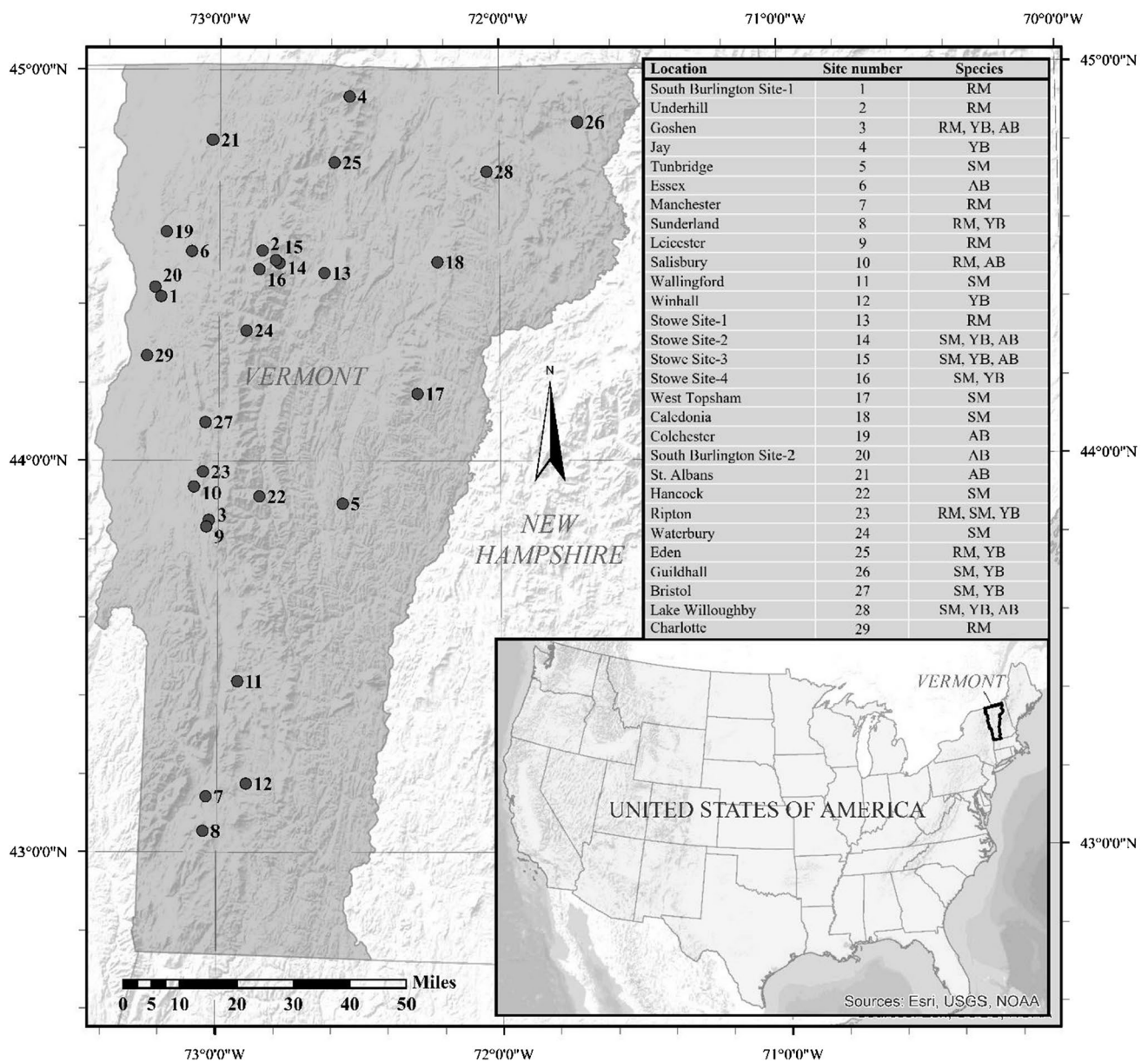


Fig. 1 Locations of the study sites throughout Vermont. SM=sugar maple, YB=yellow birch, AB=American beech, RM=red maple. Figure was created using ArcGIS 10. Base map courtesy of Esri, USGS, and NOAA

NOAA National Climatic Data Center 2018). Within this area, a total of 45 undisturbed sites of mainly dominant or co-dominant trees of our study species were selected for sampling: 12 sites each for sugar maple, yellow birch, and red maple, and nine sites for American beech. In selecting plots, we avoided managed forest areas since human disturbance can influence or mask other potential drivers of growth such as climatic or pollutant drivers. Common co-occurring dominant and co-dominant tree species varied by site and included *Quercus rubra* L., *Quercus alba* L., *Pinus strobus* L. and *Tsuga canadensis* (L.) Carrière.

Dendrochronological analysis

A total of 690 trees were sampled: 203 sugar maple, 137 American beech, 172 yellow birch, and 178 red maple (Table 1). Plots were chosen to include a broad range of northern hardwood forest locations within Vermont (Fig. 1). Within these forests, a plot center was randomly chosen and ~12 trees of the study species closest to plot center were targeted for sampling. In order to better isolate potential climate and pollution drivers for the species assessed, we focused on sampling dominant and co-dominant trees, rather than conduct a complete ecological analysis that would have

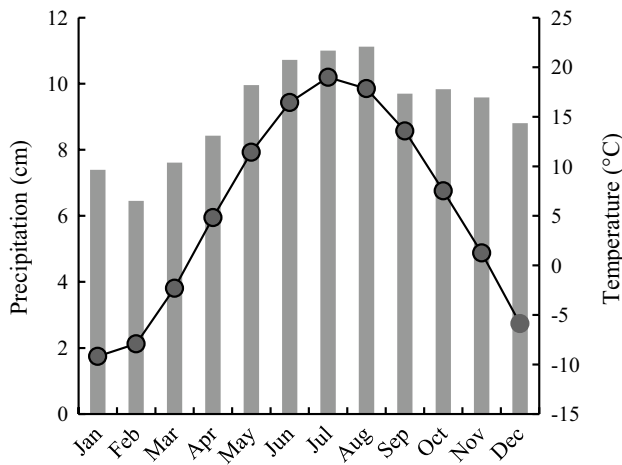


Fig. 2 Monthly mean temperature (black circles) and monthly total precipitation (grey bars) for the study area from 1945–2014 (NOAA National Climatic Data Center 2018)

included intermediate and suppressed trees. The growth of intermediate and suppressed trees could have a different climate response (Rollinson et al. 2021) and would also include trends such as those related to competition that could obscure the influence of environmental signals that we were seeking to understand. We avoided trees with serious crown or bole damage to reduce the influence of non-climatic factors on growth measurements. Trees were cored following prevailing dendrochronological techniques (Stokes and Smiley 1968): two (5 mm in diameter) xylem increment cores were collected per tree at diameter at breast height (DBH, 1.37 m above ground level), perpendicular to the slope and 180° from each other. One red maple site (Site 2) was collected by an affiliate (Kosiba et al. 2017).

Cores were prepared and measured using standard methods that are described at length elsewhere (Kosiba et al. 2017, 2018; Stern et al. 2021). Expressed population signal (EPS; cutoff of 0.80), based on the equation described by Wigley et al. (1984), was computed in the R package *dplR* (Bunn et al. 2016), and was used to determine the time period (1945 onward) during which all plot chronologies maintained a robust stand-wide signal. When an individual core occasionally correlated poorly with the master chronology (i.e., below Pearson critical correlation 99% confidence levels), it was removed from the site chronology since it indicated unusual growth trends not representative of general site growth. If a core's pith was visible, estimated tree age at breast height was assessed. If the pith was not present, core age was approximated using a pith estimator (Speer 2010) based on the curvature of the inner-most annual rings. For incomplete cores which did not exhibit curvature, age was not assessed since the pith could not be estimated.

To ascertain whether any stand-wide release events occurred throughout the chronology period, individual

Table 1 Summary of regional chronology statistics for the four study species. Statistics shown are average values for all sites within a species from detrended, standardized (67%*n* cubic smoothing spline) and prewhitened chronologies. For individual site statistics, see Tables S1–S4

| Statistic | <i>n</i> sites | <i>n</i> trees | <i>n</i> cores | Longest chronology span | Interseries correlation | Mean sensitivity | First-order autocorrelation | Mean correlation between trees | Expressed population signal | Signal-to-noise ratio |
|----------------|----------------|----------------|----------------|-------------------------|-------------------------|------------------|-----------------------------|--------------------------------|-----------------------------|-----------------------|
| Sugar maple | 12 | 203 | 398 | 1873–2014 | 0.59 | 0.3 | 0.742 | 0.505 | 0.91 | 11.7 |
| American beech | 9 | 137 | 275 | 1826–2015 | 0.56 | 0.25 | 0.781 | 0.426 | 0.89 | 11.5 |
| Yellow birch | 12 | 172 | 343 | 1740–2014 | 0.53 | 0.3 | 0.76 | 0.438 | 0.87 | 8.9 |
| Red maple | 12 | 178 | 358 | 1847–2015 | 0.53 | 0.25 | 0.753 | 0.532 | 0.89 | 12 |

tree-ring growth (raw ring width; RRW) was assessed per plot using the radial-growth averaging criteria (Nowacki and Abrams 1997) in the R package *TRADER* (Altman et al. 2014). We used a ten-year running median with a 100% threshold to identify major release events. A stand-wide release was defined as $\geq 25\%$ of all trees at a site exhibiting a major release within a decade (Nowacki and Abrams 1997).

After averaging RRW per tree, chronologies were standardized via two different methods. First, basal area increment (BAI) was calculated to assess general growth trends. BAI converts diameter increments (cm/year) into area increments (cm²/year), which minimizes size and age growth trends (West 1980). Individual site BAI chronologies were calculated and then averaged across all sites to create study-wide chronologies per species. For each species, sites were also divided into two groups based on age, size, and elevation to evaluate possible differentiations in growth based on these factors.

To relate annual growth to climate and pollution parameters, we needed a standardization method that would smooth out growth trends regarded as noise—such as the result of an episodic release—and leave in climate signals, an advantageous feature of splines (Cook and Peters 1981). Through standardization, observed RRWs are divided by the expected value of a detrended tree-ring chronology (Fritts 1976). We chose a 67%*n* cubic smoothing spline with a 50% frequency response cutoff, and then conducted autoregressive modeling on the standardized series. Autoregressive modeling removes the effects of temporal autocorrelation (first order autocorrelations), reduces the influence of endogenous disturbance, and enhances the common signal (Cook 1985), producing prewhitened (residual) chronologies. Mean annual growth values were calculated with Tukey's biweight robust mean to minimize the effect of outliers (Cook and Kairiukstis 1990) and enhance the common signal, creating a ring width index (RWI). Similar to BAI chronologies, RWI chronologies were created for each site and across all sites (per species) to create study-wide chronologies. All chronologies were truncated to the common period of 1945–2014 based on EPS calculations. Standardization and chronology building were completed using the *dplR* package in R (Bunn et al. 2016).

Environmental factors

Numerous climate parameters were considered for potential associations with growth for sugar maple, American beech, yellow birch, and red maple. To evaluate moisture metrics, we utilized data from the Standardized Precipitation–Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2017). SPEI is an index that includes precipitation and potential evapotranspiration when estimating drought; it also accounts for the effect of intensifying temperatures

on water demand (Vicente-Serrano et al. 2010). SPEI values were acquired for individual sites and averaged to create a region-wide SPEI dataset at 1-month (SPEI01) and 3-month (SPEI03) time steps. The 1-month time step enabled us to more closely pinpoint specific times of influence within a season, while the 3-month time step allowed us to evaluate moisture on a seasonal level.

To assess temperature variables, we obtained climate data from the National Climatic Data Center (NOAA National Climatic Data Center 2018). We used divisional climate data because climate divisions could synthesize climate characteristics across the state of VT, versus individual climate stations which may record locally specific weather phenomena and which also had gaps in the data. We evaluated two variables within this dataset: monthly maximum temperature (T_{\max}) and monthly minimum temperature (T_{\min}). From these variables we also created additional date-specific categories for previous Summer (pJune–pAugust), previous Fall (pSeptember–pNovember), Winter (pDecember–current February), Spring (March–May), Summer (June–August), Fall (September–November), and Water year (pOctober–current September). We also applied two heat indices: cooling degree days (CDD) and heating degree days (HDD). CDD measures high temperature exposure, computed as the number of degrees that average daily temperature is above 18.3° C (65° F). Conversely, HDD gauges low temperature exposure, calculated as the number of degrees that daily average temperature is below 18.3° C (65° F). While CDD and HDD were invented for estimating building cooling and heating needs, they have also been associated with tree growth and physiology, and can serve as proxies for accumulated high and low temperature exposure over time (e.g., Kosiba et al. 2018). We were also interested in correlating growth with snowpack data. Since data of actual depth of monthly snowpack were not readily available, we used two surrogate metrics from the same NOAA data source: number of days in a month that snow depth was greater than 2.54 cm (hereafter referred to as snow duration), and monthly snowfall (mm). Pollution deposition data (SO₄²⁻, NO₃⁻, cation to anion ratio, and rainfall pH) were acquired from the National Atmospheric Deposition Program (National Atmospheric Deposition Program 2017) for two sites in VT: Bennington and Underhill. Data were also obtained from the Hubbard Brook Ecosystem Study in New Hampshire (Likens 2016). To extend the VT data back further, data from the sites in VT (1982–2014) were averaged and regressed against pollutant deposition data from New Hampshire (1980–2012). The total timespan for this expanded dataset was 1980–2014.

Statistical analyses

To understand associations between environmental variables and tree growth, we conducted stationary correlation

functions using Pearson's correlations via bootstrap resampling (1,000 bootstrap samples; Biondi and Waikul 2004) using the R package *treeclim* (Zang and Biondi 2015). These correlations were between monthly, seasonal, and water year climate data and the RWI regional chronologies (1945–2014). Monthly correlations extended 18 months from previous year's June through current year's October to account for integrated and lagged effects. Correlations over the entire chronology allowed us to evaluate associations of growth and environmental factors regardless of the stage of stand development (i.e., maturing versus mature forest). To explore potential changes over time, we also evaluated climate-growth correlations prior to (1945–1979) and after 1980 (1980–2014)—a division that provided an equal sample size for group comparisons, and coincided with the timing of the onset of sugar maple decline in the region that could account for reductions in sugar maple growth or increases in the growth of competing species (Houston 1999). Pollutant deposition data was not available for the entire period of 1945–1979; thus, we conducted monthly, seasonal, and water year pollution deposition correlations with deposition data only for the 1980–2014 period. To understand any possible variations in climate response based on site features, we also conducted correlations between two elevation groups, divided by the median elevation for each species. Median elevations were as follows: sugar maple—542 m, American beech—282.2 m, yellow birch—466 m, and red maple—368 m.

Results

Chronology statistics

The average interseries correlations and mean sensitivities of our four regional species chronologies did not differ greatly (Table 1). Sites had an estimated median age range of 62.5 to 190.0 years; yellow birch had both the youngest and oldest median site age (Tables S1–S4). Sites exhibited a mean DBH range of 35.5–38.7 cm (Tables S1–S4); American beech were the smallest trees and red maple were the largest trees.

Basal area increment growth trends

From 1945 to 2014, BAI growth for all four species increased during stand maturation and leveled off during the second half of the chronology (Fig. 3). Maximum growth for each species was: sugar maple 17.7 cm² in 2008 and 2009, American beech 16.2 cm² in 2009, yellow birch 17.3 cm² in 2009, and red maple 18.5 cm² in 1980 (Fig. 3). Four of the 45 plots assessed showed evidence of limited release events of unknown origin.

To assess whether growth among stands differed based on tree size, age or elevation, sites were partitioned into two equal groups based on mean tree size (DBH), median age, and elevation per site. For sugar maple, American beech and red maple, there were no differences among sites in BAI slope over the chronology (1945–2014) attributable to these three stand characteristics. For yellow birch, younger (< 107 years) sites had a significantly higher rate of growth than older sites ($t=2.69$; $P=0.03$), as did sites with smaller trees (< 35.9 cm) as compared to sites with larger trees ($t=2.65$; $P=0.03$).

Climate and deposition correlations with growth

Sugar maple

Sugar maple exhibited positive correlations with winter moisture availability throughout the chronology (1945–2014), which were evident as associations in early winter (December SPEI01; $r=0.35$, $P\leq 0.01$), as well as the entire winter (February SPEI03; $r=0.26$, $P\leq 0.05$) (Fig. 4a). These winter variables were significant regardless of time period or elevation (Tables S5a and S6a). Summer moisture was also positively associated with sugar maple growth, as indicated by associations with June SPEI01 ($r=0.26$, $P\leq 0.05$) and August SPEI03 ($r=0.31$, $P\leq 0.05$).

Correlations with temperature (1945–2014) were less numerous than those with moisture. Sugar maple growth was negatively correlated with pJuly CDD, a measure of accumulated heat ($r=-0.26$, $P\leq 0.05$). Growth was also negatively associated with March T_{\max} ($r=-0.29$, $P\leq 0.01$) and positively associated with March HDD, a measure of accumulated cold ($r=0.26$, $P\leq 0.05$). In the 1980–2014 period, multiple negative associations with warmer temperatures in pNovember appeared (Table S5a). The only association found with pollution deposition was a positive correlation with pAugust cation to anion ratios (1980–2014; $r=0.28$, $P\leq 0.05$).

American beech

Only one moisture variable was significantly associated with American beech growth for the entire chronology: pDec SPEI01 ($r=0.32$, $P\leq 0.05$) (Fig. 4b). This correlation appeared to be strongly influenced by a response across more recent decades ($r=0.41$, $P\leq 0.01$; Table S5b) and higher elevation sites ($r=0.33$, $P\leq 0.01$; Table S6b). For temperature, beech exhibited negative correlations with pAugust T_{\max} ($r=-0.33$, $P\leq 0.01$), HDD ($r=0.30$, $P\leq 0.05$), and CDD ($r=-0.30$, $P\leq 0.05$; Fig. 4b). Overall, beech was also negatively correlated with January HDD ($r=0.25$, $P\leq 0.05$); for trees at lower elevations, negative correlations with Jan T_{\min} and Jan T_{\max} were also evident (Table S6b).

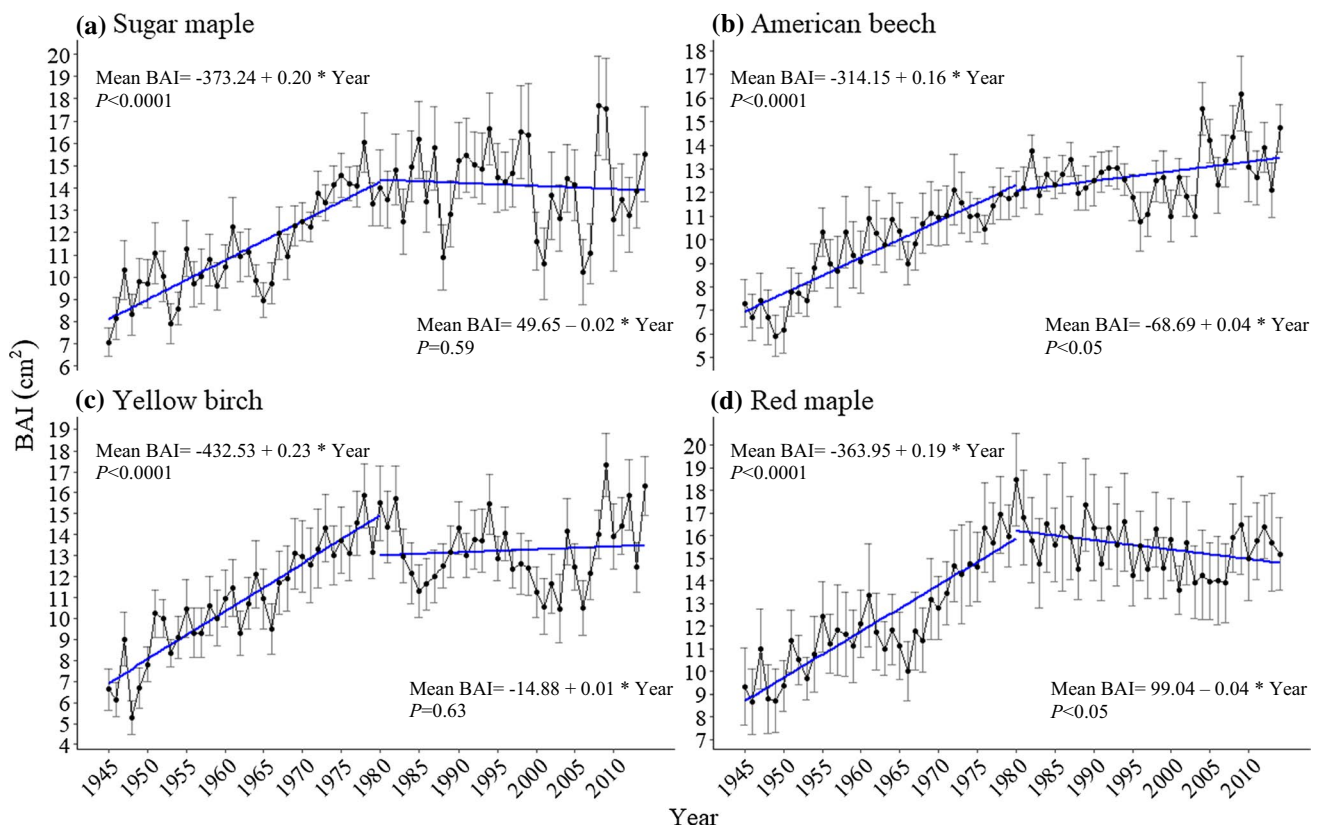


Fig. 3 Mean BAI growth (\pm SE) from 1945 to 2014 for four species: **a** sugar maple, **b** American beech, **c** yellow birch and **d** red maple. The linear regression of growth over time (dotted line and the asso-

ciated equation) is depicted. For all four species, we saw increasing growth followed by plateaued growth indicative of a maturing forest

American beech growth showed negative associations with warmer temperatures at the beginning of summer (June T_{\max} ; $r = -0.33$, $P \leq 0.01$ and June HDD; $r = 0.30$, $P \leq 0.05$) and the entire summer season (summer T_{\max} ; $r = -0.34$, $P \leq 0.01$ and summer HDD: $r = 0.27$, $P \leq 0.05$; Fig. 4b). American beech exhibited no significant correlations with pollutant deposition parameters.

Yellow birch

Yellow birch growth showed numerous positive correlations with previous year moisture availability parameters, including pAugust SPEI01 ($r = 0.30$, $P \leq 0.01$), pOctober SPEI03 ($r = 0.26$, $P \leq 0.05$), and pDecember SPEI03 ($r = 0.25$, $P \leq 0.05$) (Fig. 4c). The association with pDecember SPEI03 was particularly evident in the first half of the chronology ($r = 0.40$, $P \leq 0.01$; Table S5c) and at higher elevation sites ($r = 0.30$, $P \leq 0.05$; Table S6c). Summer moisture in the current year was also an important metric for yellow birch. Growth (1945–2014) was positively correlated with August SPEI03 ($r = 0.25$, $P \leq 0.05$), the relationship likely influenced by the first half of the chronology ($r = 0.39$, $P \leq 0.01$;

Table S5c) and higher elevation sites ($r = 0.30$, $P \leq 0.05$; Table S6c).

For temperature, yellow birch growth was negatively correlated with pAugust T_{\max} ($r = -0.39$, $P \leq 0.01$), CDD ($r = -0.34$, $P \leq 0.01$), and pSeptember T_{\max} ($r = -0.25$, $P \leq 0.05$) and positively correlated with HDD ($r = 0.30$, $P \leq 0.01$). Of all species, yellow birch exhibited the most numerous associations with pollution deposition variables; in the second half of the chronology, yellow birch growth correlated negatively with April NO_3^- ($r = -0.33$, $P \leq 0.05$) and positively with numerous cation to anion ratio variables, including those for winter ($r = 0.38$, $P \leq 0.05$) and spring ($r = 0.35$, $P \leq 0.05$; Fig. 4).

Red maple

Red maple growth (1945–2014) was positively associated with multiple summer moisture metrics: June SPEI01 ($r = 0.30$, $P \leq 0.01$), July SPEI01 ($r = 0.28$, $P \leq 0.05$), July SPEI03 ($r = 0.29$, $P \leq 0.05$), and August SPEI03 ($r = 0.31$, $P \leq 0.01$) (Fig. 4d). Associations with summer moisture were particularly influenced by lower elevation sites, which showed numerous significant correlations with moisture in

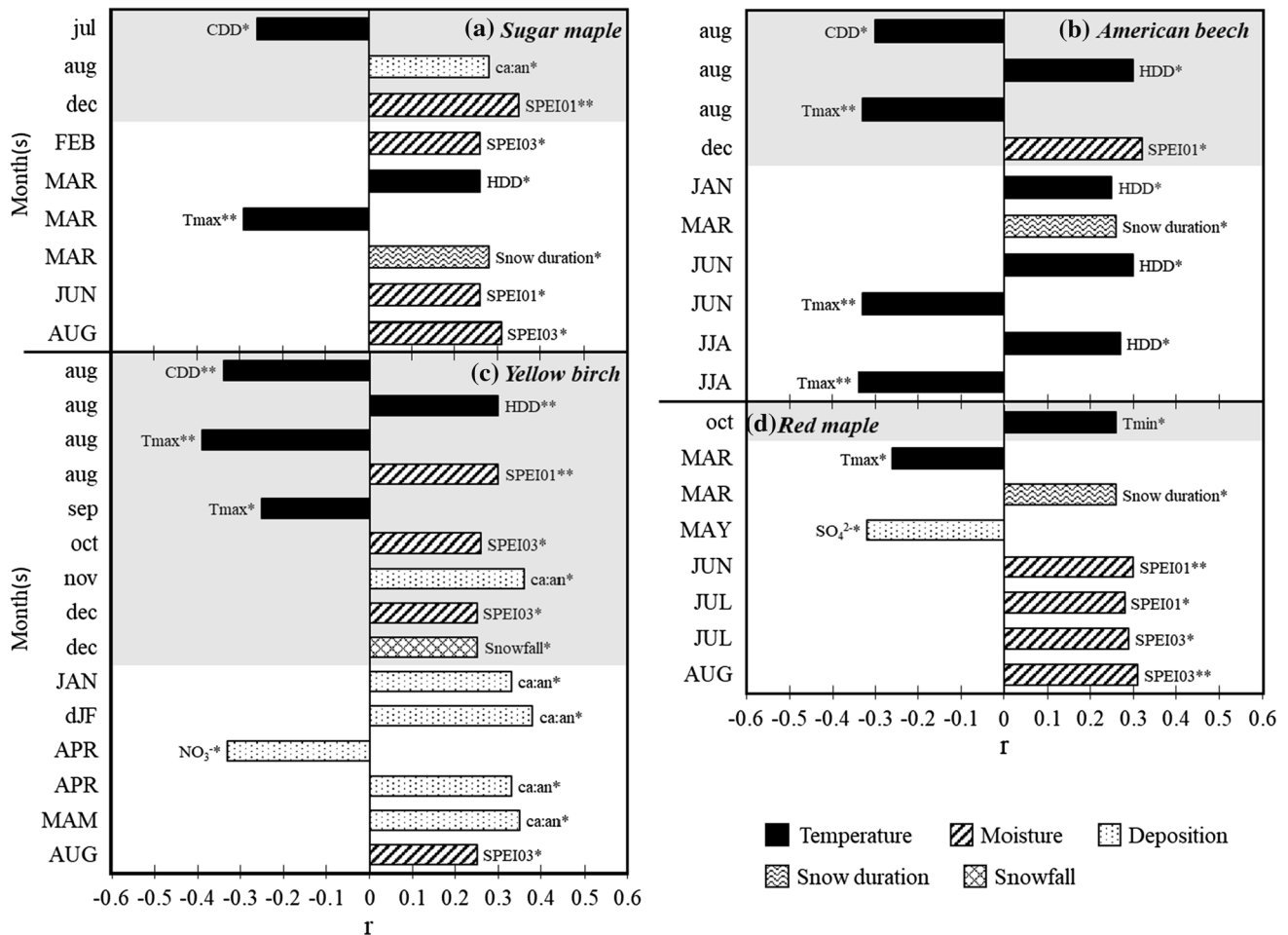


Fig. 4 Significant climate- (1945–2014) and deposition- (1980–2014) growth (ring width index) correlation coefficients for **a** sugar maple, **b** American beech, **c** yellow birch, and **d** red maple. Lower case letters and shaded areas specify previous year's months. JJA=current year's June, July, and August: pooled to create a summer variable; dJF=previous year's December and current year's January and February, grouped to create a winter variable; MAM=current year's March, April and May: grouped to create

May through August (Table S6d). For temperature, pOctober T_{\min} correlated positively with red maple growth ($r=0.26$, $P\leq 0.05$), and March T_{\max} showed a negative correlation ($r=-0.26$, $P\leq 0.05$) (Fig. 4d). For pollutant deposition variables, red maple exhibited a negative correlation with May SO_4^{2-} in the second half of the chronology ($r=-0.32$, $P\leq 0.05$).

Snow data

Considering significant correlations between growth and winter moisture for sugar maple, American beech, and yellow birch, we were interested in conducting additional correlations with snow data to assess the possibility that it was this form of precipitation that was affecting growth.

a spring variable. T_{\max} =maximum temperature, T_{\min} =minimum temperature, CDD=cooling degree days, HDD=heating degree days, SPEI=Standardized Precipitation-Evapotranspiration Index, ca:an=cation to anion ratio, SO_4^{2-} =sulfate deposition. Note that "snow duration" was the number of days in a month that snow depth was at least 2.54 cm. For further explanation on variables, see Methods. Significance levels: * $P<0.05$; ** $P<0.01$

Significant positive correlations were present between growth and number of days that snow depth was greater than 2.54 cm in the month of March for sugar maple ($r=0.28$, $P\leq 0.05$), American beech ($r=0.26$, $P\leq 0.05$), and red maple ($r=0.26$, $P\leq 0.05$). Yellow birch showed a positive correlation with pDecember snowfall ($r=0.25$, $P\leq 0.05$), similar to its correlation with pDecember SPEI03. Associations between growth and snow data across elevations and time periods were more numerous and included previous December snowfall (sugar maple, American beech and yellow birch), winter snowfall (yellow birch) and the number of days with at least 2.54 cm of snow on the ground in December (yellow birch) and March (sugar maple, American beech and red maple) (Tables S5, S6).

Discussion

Growth trends

BAI growth patterns of all four species—sugar maple, American beech, yellow birch, and red maple—displayed two distinct periods: a maturing forest showing steady increases in growth, followed by plateaued growth indicative of a mature forest (Fig. 3). This is the expected growth pattern as trees get larger (Weiner and Thomas 2001) such as in forests recovering from historic land clearing in the northeastern US (Foster 1995). In the Northeast, sugar maple has exhibited a slowed rate of basal area growth (Pontius et al. 2016) similar to our findings, but also negative growth trends in the Adirondack mountains of New York (Bishop et al. 2015), unlike what we found in VT. While American beech generally showed only modest growth, rates appear to have increased in recent years (Fig. 3). This apparent increase occurred despite the prevalence of beech bark disease—an insect-disease complex that reduces the woody growth of affected trees (Gavin and Peart 1993). However, because we sampled trees with little evidence of beech bark disease, we had a reduced capacity to detect disease-related growth declines. Still, our beech findings agree with those of Pontius et al. (2016), who found an increase in radial growth for mature beech trees (> 25.4 cm DBH) in New Hampshire, particularly in recent years. Yellow birch sites in our study exhibited variable but sustained growth over the past several decades. Growth for this species has been inconsistent in locations across the region: Pontius et al. (2016) found an increase in biomass of mature yellow birch trees in New Hampshire, but overall reduced basal area due to a lack of regeneration. van Doorn et al. (2011) found that yellow birch experienced the greatest reduction in biomass as compared to other species at the Hubbard Brook Experimental Forest—a reduction that resulted from high mortality and a lack of recruitment. These differing results are consistent with the greater variability among yellow birch growth that we observed when compared to American beech and red maple, and support the idea that yellow birch growth differs across elevations and locations (Pontius et al. 2016). Red maple had the highest average growth across the chronology of any species that we assessed, though growth decreased from maximum levels in recent years (Fig. 3). Red maple has increased in both basal area and abundance in New Hampshire, which has been attributed to the species' capacity to outcompete co-occurring species because of its characteristics as an ecological generalist with great physiological plasticity (Pontius et al. 2016). Its growth in Canada has also been found to increase with latitude, suggesting that this species is less limited by low temperature than other factors, such as disturbance history (Zhang et al. 2015).

Correlations with moisture

For all four species, moisture exhibited a positive relationship with growth over the past 70 years. Contrary to portions of our H_1 hypothesis, this was even evident for red maple, which is an environmental generalist that grows over a wide range of moisture conditions (Burns and Honkala 1990). The three classic species of the northern hardwood forest (sugar maple, American beech, and yellow birch) showed a greater number of correlations with moisture in the first half of their chronologies (1945–1979) than the second (Table S5). During this time, the region experienced a major drought (1964–1967; NOAA National Centers for Environmental Information 2018). Conversely, more recent decades have seen an unparalleled increase in precipitation (Pederson et al. 2013), possibly explaining the weaker moisture signal in the second half of the chronologies. Lack of drought in recent years has been used to explain the reduced sensitivity of tree rings to soil moisture in the Midwest US (Maxwell et al. 2016), so this may be a more widespread phenomenon.

Summer moisture availability showed significant associations with growth for all species, although for American beech, this was only evident at lower elevations and during the first half of the chronology (Table S5b and S6b)—possibly suggesting a lesser sensitivity for this species. Positive correlations of radial growth with summer precipitation have been noted by others for sugar maple and American beech (Tardif et al. 2001), although Takahashi and Takahashi (2016) found no significant climate-growth correlations for beech at all in eastern Canada. For yellow birch also in Canada, Kwiaton and Wang (2015) found positive associations between growth with both current and previous-year's precipitation levels, whereas Zarnovican (2000) found significant associations with precipitation for only one of three sites evaluated. For red maple, growing season precipitation has been shown to correlate significantly with growth in the Appalachian Mountains (Fekedulegn et al. 2003), and was also the only climate variable that improved growth models of this species' basal area development in the midwestern US (Pszwaro et al. 2016). Our findings are in line with larger-scale studies showing the dominating importance of growing season moisture on broadleaf trees in the northeastern US (Martin-Benito and Pederson 2015; D'Orangeville et al. 2018) and Europe (e.g., Mette et al. 2013). Along with correlations with current summer moisture, each species showed associations with previous summer moisture in at least one time period or elevational grouping. This is consistent with a possible “legacy effect” of environmental conditions one year affecting growth the next, presumably through influences on stored carbohydrates used to fuel early growth (Kosiba et al. 2018).

While many tree species showed a link with growing season moisture, what was most notable in our study were the

numerous significant correlations with moisture availability in the non-growing season. Winter moisture availability was positively associated with growth for the three classic northern hardwood species. While these species showed associations with multiple winter moisture metrics, all three were linked with moisture levels during the previous December, underscoring the key role of moisture in early winter, presumably in the form of snow. Kosiba et al. (2017) also found previous December moisture to be positively associated with sugar maple and yellow birch growth in VT, and Zarnovican (2000) noted this for yellow birch in Canada.

We explored whether this association with winter moisture was also seen with snow data and found that all four species exhibited a positive correlation with at least one of the snow metrics (Fig. 4). Indeed, positive correlations with snow data were among the most consistent factors associated with growth across the species. The months with positive correlations with snow data did not always correspond to the months (primarily December) when positive winter moisture correlations were so prevalent. However, we suspect that this discrepancy is because we did not have actual measures of snowpack, but instead worked with other surrogate datasets.

Snowpack provides an essential function in winter because it acts as a potent insulator of forest soils, buffering them from low air temperatures that can lead to soil freezing (Hennon et al. 2012). Considering this, insufficient snowpack can increase the risk of soil freezing and associated root freezing injury and loss (Cleavitt et al. 2008). This can then disrupt tree carbon relations and reduce above-ground growth (Comerford et al. 2013). Although noted for multiple tree species and locations (e.g., Hennon et al. 2012), this chain of events has been particularly well documented for sugar maple in the northeastern US (Tierney et al. 2001; Comerford et al. 2013; Reinmann et al. 2019). Long-lasting freeze–thaw events may be particularly detrimental to sugar maple growth (Moreau et al. 2020). Our positive correlations between winter moisture and snow with sugar maple growth are consistent with the well-established connections between snowpack, soil freezing, root injury and growth for this species.

Beyond sugar maple, our data suggest that all species assessed showed signs of sensitivity to winter moisture or snow. This was not surprising for yellow birch, which has also been reported to be sensitive to root freezing injury associated with low snowpacks and soil freezing (Zhu et al. 2000, 2002; Tierney et al. 2001). However, to our knowledge, this has not been reported before for American beech. For red maple in our study, positive correlations with winter moisture were more limited and restricted to March snow data. Snow manipulation studies involving red maple have shown that reduced snowpack can increase root injury, which is then associated with delayed leaf-out (Sanders-DeMott et al. 2018a), reduced nitrogen uptake capacity

(Sanders-DeMott et al. 2018b) and can even counteract the positive influence of warmer growing seasons on leaf-level photosynthesis (Harrison et al. 2020). However, other work has indicated that reduced snowpack can stimulate red maple radial growth, at least in the short-term (Reinmann and Timpler 2016). At a minimum, associations between snowpack and red maple physiology and growth appear to be more nuanced than the more consistent relationships noted for other northern hardwood species.

Our findings, which highlight the key role of moisture in both the growing and non-growing seasons raise questions about the impacts of future hydrological regimes within the Northeast. Precipitation in the northeastern US has been increasing over the past several decades and is projected to increase further (Janowiak et al. 2018). While increases in annual precipitation may seem promising for tree growth, the seasonality of water availability must be considered since future precipitation is not expected to increase uniformly across all seasons; winter and spring are projected to experience the greatest rises in precipitation (Janowiak et al. 2018). However, models show that as the twenty-first century progresses, winter precipitation will likely fall increasingly in the form of rain as opposed to snow (Demaria et al. 2016). In contrast, summer is not expected to show an increase (Lynch et al. 2016) and may even exhibit decreases in precipitation (Janowiak et al. 2018)—a phenomenon that could jeopardize the growth potential of iconic northern hardwood species.

Correlations with temperature

Across the full chronology, species differed in the number of significant correlations with temperature, with American beech showing the most (six), followed by yellow birch (four), sugar maple (three) and red maple (two). This may reflect a differing sensitivity of these species to projected temperature increases with climate change. Nonetheless, there were fewer significant correlations with temperature than with moisture metrics, which is consistent with hypothesis H₂. While all moisture metrics displayed positive relationships with growth, most measures of temperature illustrated negative associations, with a few exceptions. Growth of the three typical northern hardwood species showed a negative relationship with previous summer or fall temperatures. In contrast, red maple showed a positive relationship with previous summer and fall temperatures. In another VT study with a far more restricted sampling area, similar patterns between sugar maple and previous summer temperatures were evident, although red maple exhibited the opposite association (Kosiba et al. 2017). In our study, both sugar and red maple had negative relationships with warmer spring temperatures.

Just as winter moisture showed a notable connection to growth, winter temperatures were significant for the three quintessential northern hardwood species. Beech growth had negative associations with warmer winter temperatures throughout the entire time period, while yellow birch exhibited this trend only in more recent decades. The negative association we observed between sugar maple growth and previous November temperatures (Table S5a) was similar to Takahashi and Takahashi (2016), who found negative correlations between sugar maple growth and previous December temperatures in eastern Canada. Tardif et al. (2001) also found negative correlations between sugar maple growth and mild late winters (February–March) in southwestern Quebec. Throughout the last century in the Northeast, the season with the greatest observed increases in temperature was winter, where minimum temperatures increased even more than maximum temperatures (Janowiak et al. 2018). In the second half of their chronologies, the three classic northern hardwood species all had negative associations with maximum and minimum temperatures in either late previous fall (November) or in winter (Table S5a–c). In contrast, red maple displayed a positive relationship with warmer winter temperatures at higher elevations (Table S6b), suggesting that less extreme winter temperatures may benefit this species at some locations.

Numerous negative associations between summer temperatures and growth were evident for all species except red maple, suggesting a wide-spread sensitivity to high temperatures that can cause heat-induced moisture limitations or more directly limit growth through increases in respiration (Rennenberg et al. 2006; Stern et al. 2021). However, this apparent influence was not uniform. For example, during the first half of their chronologies, sugar maple and yellow birch showed positive relationships with warmer minimum summer temperatures, although this correlation disappeared in more recent decades when temperatures increased. Interestingly, red maple showed this positive relationship with minimum summer temperatures at high elevation sites throughout its chronology, another indication that rising temperatures may benefit this species at higher locations where temperatures may otherwise constrain growth. In contrast, red maple at low elevations showed negative relationships with warmer summer temperatures, suggesting a sensitivity to heat stress at locations where high summer temperatures are more likely. Except for occasionally being influential to red maple, elevation was not generally an important modulator of growth for the northern hardwood species that we assessed (hypothesis H₄).

Correlations with pollution deposition

Significant deposition-growth correlations, while less numerous than ones with moisture and temperature, were evident for all species except American beech, which is in alignment with our hypothesis H₃. Consistent with these findings, much work has documented that sugar maple can experience growth declines following pollution-induced cation imbalances (e.g., Schaberg et al. 2001, 2010; Juice et al. 2006), and some evidence points to the pollution sensitivity of yellow birch (Halman et al. 2014). Furthermore, our findings of no significant correlations between beech growth and pollution deposition are consistent with its documented insensitivity to acid deposition (Halman et al. 2014). Similar findings for European beech (*Fagus sylvatica* L.) (Bosela et al. 2018) may suggest that an insensitivity of growth to pollution inputs may be a more general characteristic of the genus. However, it was somewhat surprising that red maple growth was negatively correlated with pollution inputs since it is not a species reported to experience pollution-induced decline (Driscoll et al. 2001; Schaberg et al. 2010). This may showcase a previously unrecognized vulnerability of a species that otherwise seems to be thriving (Abrams 1998). Nonetheless, the relatively few numbers of correlations with pollution deposition overall are logical since pollutant levels are generally declining in the northeastern US (Siemion et al. 2018) since the implementation of the Clean Air Act (1990) and thus, should have less of an impact on growth.

Conclusions

Moisture availability in the summer months was important for all four species we examined, which contributes further evidence to recent broad-scale studies that highlight the importance of growing season moisture regimes in sustaining woody productivity. However, this apparent influence was less evident for American beech, suggesting a lesser vulnerability for this species. More precipitation/snow in winter also appeared helpful in promoting radial growth. Indeed, snow seemed to have a broader influence on tree growth beyond the well documented evidence for sugar maple—here also showing relevance to yellow birch, American beech, and even somewhat red maple. Considering the overwhelmingly positive influence of adequate moisture for maintaining growth, changes in the amount, form (rain versus snow), intensity (increasing runoff versus allowing for soil penetration), and periodicity of precipitation beyond contemporary norms could threaten optimal growth within the northern hardwood forest.

All species showed negative associations between growth and temperature the year before or concurrent with the year of xylem formation. However, the number of these

correlations differed among species, with American beech showing the most, red maple the least, and yellow birch and sugar maple being intermediate. This provides further evidence of differential impacts on growth and competition as temperatures rise.

Perhaps what was most notable from our study was the consistent sensitivity of the three archetypal northern hardwood species to winter moisture and temperature regimes. This may be due to the interconnection between winter snowpacks, soil freezing and the potential for root damage that alter tree carbon relations—phenomena that have been well documented at specific sites but require further study to verify their broader relevance. Although many modeling efforts focus on winter temperatures' influence on tree species performance, our findings suggest that winter precipitation may be another factor to consider in determining future habitat suitability for tree species adapted to cold climates. Red maple growth did not show a negative association with winter temperature and relationships to snow data were more limited. Instead, red maple showed a positive association with warmer winter and even summer temperatures at some locations. These responses were unique among the species we examined, which supports the possibility that red maple may be less vulnerable to changes in the climate than some co-occurring species.

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