

Eastern white pine and eastern hemlock growth: possible tradeoffs in response of canopy trees to climate

Rebecca L. Stern, Paul G. Schaberg, Shelly A. Rayback, Paula F. Murakami, Christopher F. Hansen, and Gary J. Hawley

Abstract: A warming climate and extended growing season may confer competitive advantages to temperate conifers that can photosynthesize across seasons. Whether this potential translates into increased growth is unclear, as is whether pollution could constrain growth. We examined two temperate conifers — eastern white pine (*Pinus strobus* L.) and eastern hemlock (*Tsuga canadensis* (L.) Carrière) — and analyzed associations between growth (476 trees in 23 plots) and numerous factors, including climate and pollutant deposition variables. Both species exhibited increasing growth over time and eastern white pine showed greater maximum growth. Higher spring temperatures were associated with greater growth for both species, as were higher autumnal temperatures for eastern hemlock. Negative correlations were observed with previous year (eastern hemlock) and current year (eastern white pine) summer temperatures. Spring and summer moisture availability were positively correlated with growth for eastern white pine throughout its chronology, whereas for hemlock, correlations with moisture shifted from being significant with current year's growth to previous year's growth over time. The growth of these temperate conifers might benefit from higher spring (both species) and fall (eastern hemlock) temperatures, though this could be offset by reductions in growth associated with hotter, drier summers.

Key words: dendrochronology, temperate conifers, temperature, moisture, climate change.

Résumé : Un climat plus chaud et une saison de croissance plus longue pourrait conférer des avantages compétitifs aux conifères de la zone tempérée chez qui la photosynthèse peut se poursuivre en toute saison. Il n'est pas clair si cette possibilité pourrait se traduire par une croissance accrue et de même si la pollution pourrait limiter la croissance. Nous avons étudié deux conifères de la zone tempérée : le pin blanc (*Pinus strobus* L.) et la pruche du Canada (*Tsuga canadensis* (L.) Carrière), et nous avons analysé les liens entre la croissance (476 arbres dans 23 places échantillons) et plusieurs facteurs, incluant des variables liées au climat et aux retombées de polluants. Les deux espèces ont augmenté leur croissance avec le temps et le pin blanc a connu la croissance maximum la plus élevée. Les températures printanières élevées étaient associées à une plus forte croissance chez les deux espèces, ainsi que les températures automnales élevées dans le cas de la pruche du Canada. Des corrélations négatives ont été observées avec les températures estivales de l'année précédente (pruche du Canada) et de l'année en cours (pin blanc). La disponibilité d'humidité au printemps et à l'été était positivement corrélée avec la croissance du pin blanc tout au long de sa chronologie, tandis que dans le cas de la pruche du Canada les corrélations avec l'humidité allaient avec le temps de significatives avec la croissance de l'année en cours à celle de l'année précédente. La croissance de ces conifères de la zone tempérée pourrait bénéficier de températures plus chaudes au printemps (les deux espèces) et à l'automne (pruche du Canada), bien que cela puisse être compensé par des réductions de croissance associées à des étés plus chauds et plus secs. [Traduit par la Rédaction]

Mots-clés : dendrochronologie, conifères de la zone tempérée, température, humidité, changement climatique.

Introduction

Forest composition and growth may shift as the suitability of habitats for component tree species shifts with climate change (Prasad et al. 2007 — ongoing). For species in temperate forest communities that have adapted to existing seasonal differences in temperature and precipitation types, alterations in climate could have profoundly negative effects on tree health and productivity (e.g., Reinmann et al. 2019). While warmer temperatures may be unfavorable to many species, one taxon, conifers, may actually benefit. Temperate evergreen conifers have the ability to photosynthesize across seasons if conditions are suitable, because they maintain their needles throughout the year (Schaberg

et al. 1995; Hadley 2000). However, the ability for photosynthetic gain outside of the growing season may not necessarily translate into increased growth because changes in growing season climate could limit carbon (C) gain — effectively nullifying gains due to increased photosynthesis at other times. Recent evidence of increased growth, at least partially related to an extended growing season, has been observed for one temperate conifer in the Northeast — red spruce (*Picea rubens* Sarg.) (Kosiba et al. 2018; Mathias and Thomas 2018). Whether this phenomenon is unique to red spruce or is more broadly applicable to other ecologically and economically important temperate conifers in the region, such as eastern white pine (*Pinus strobus* L.) and eastern hemlock (*Tsuga canadensis* (L.) Carrière), has not yet been explored. Studying

Received 3 December 2020. Accepted 20 February 2021.

R.L. Stern,* C.F. Hansen, and G.J. Hawley. Rubenstein School of Environment and Natural Resources, The University of Vermont, Burlington, VT 05405, USA.

P.G. Schaberg and P.F. Murakami. Northern Research Station, Forest Service, US Department of Agriculture, Burlington, VT 05405, USA.

S.A. Rayback. Department of Geography, The University of Vermont, Burlington, VT 05405, USA.

Corresponding author: Rebecca L. Stern (email: rebecca.stern@erm.com).

*Present address: ERM, Malvern, PA 19355, USA.

© 2021 The Author(s). Permission for reuse (free in most cases) can be obtained from copyright.com.

the growth and response of both eastern white pine and eastern hemlock may offer insight into a possible general response of temperate conifers to a changing climate in the region.

Eastern white pine grows primarily in the northeastern United States (US), extending west to Minnesota, south to Georgia (mostly in the Appalachian Mountains), and north into southern Canada (NAPA 2014). In the pre-European settlement forests of the northeastern US, eastern white pine was a minor component (Cogbill 2000), though it was distributed widely and occurred in a range of topographic positions and moisture conditions (Abrams 2001). Eastern white pine has doubled in its frequency across New England in response to a decrease in harvesting and regrowth on abandoned agriculture land (Cogbill 2000).

Eastern hemlock is a foundation species in forests of the eastern US (Ellison 2014) that can grow in a wide range of sites, although it appears most competitive in cool, moist environments with little historical disturbance (Foster et al. 2014). Over a large portion of its range, the prevalence and growth of eastern hemlock have been significantly reduced due to feeding damage by a non-native insect — the hemlock woolly adelgid (HWA: *Adelges tsugae* Annand) (e.g., Nuckolls et al. 2009). While HWA is present in parts of southern Vermont (USDA Forest Service 2019), success of this insect has been limited in the northern part of eastern hemlock's range, in part because overwintering mortality of the insect has restricted its spread there (Ellison et al. 2018). With increasingly warmer winters, HWA are likely to experience higher overwinter survival and expand into the northern range of eastern hemlock (McAvoy et al. 2017). However, eastern hemlock survival rates have been shown to average 73% after 15 years of the pest's introduction to a site (Eschtruth et al. 2013), and tree mortality may be slower to occur in northern forests due to low temperature constraints on HWA population growth (Paradis et al. 2008). Even with HWA infestation, eastern hemlock may still have great potential for C capture and growth within the northern forest.

The purpose of this study was to evaluate patterns and potential climate and pollution drivers of growth for eastern white pine and eastern hemlock in the northern forest. The influence of pollution was assessed because acid deposition has reduced the growth of multiple ecologically significant species in the region, most notably another temperate conifer — red spruce (DeHayes et al. 1999; Driscoll et al. 2001; Schaberg et al. 2010). Our objectives for this study were to (i) describe and compare long-term growth patterns of these two species, (ii) examine radial growth associations of both species to climate factors, (iii) analyze potential growth responses to pollutant deposition, and (iv) investigate potential differences in climate- and deposition-growth associations over time to better understand which environmental variables best explain growth in this region. To address these objectives, we sampled 476 dominant and co-dominant canopy class eastern white pine and eastern hemlock trees at 23 plots throughout Vermont (VT), and analyzed tree-ring growth in relation to tree and stand characteristics, as well as climate and pollution data.

Methods

Study area

The study area is located throughout the state of VT, ranging from 42.75°N to 44.93°N and 72.37°W to 73.36°W (Fig. 1). Mean annual precipitation is 112 cm, with 46% of precipitation falling during the growing season, from May through September (NOAA National Climatic Data Center 2019). Mean temperature is warmest in July (25.6 °C) and coldest in January (−14.5 °C; Fig. 2). Within this geographic range, 23 forested plots were selected for sampling: eight with only eastern white pine, 10 with only eastern hemlock, and five plots with both species. With the exception of three eastern hemlock sites that were considered old growth with no evidence of land clearance, these sites were second-

growth stands recovering from deforestation and intensive land use during the late 19th and early 20th centuries. Because human disturbance can impact or obfuscate the influence of environmental factors (e.g., changes in temperature, moisture, and pollution deposition) on growth, we avoided currently managed forests when selecting plots. We were not selective in picking sites with specific intrinsic characteristics such as aspect, soil type or elevation. Rather, we were interested in choosing sites that would provide a broad representation of mature canopy trees of each species. Soil parent material across sites ranged from loamy lodgement and supraglacial tills to sandy glaciofluvial or clayey glaciolacustrine deposits (USDA Natural Resources Conservation Service 2019). Other common canopy tree species varied per site but included *Acer saccharum* (Marsh), *Fagus grandifolia* (Ehrh.), *Betula alleghaniensis* (Britton), *Quercus rubra* (L.), and *Acer rubrum* (L.).

Dendrochronological techniques

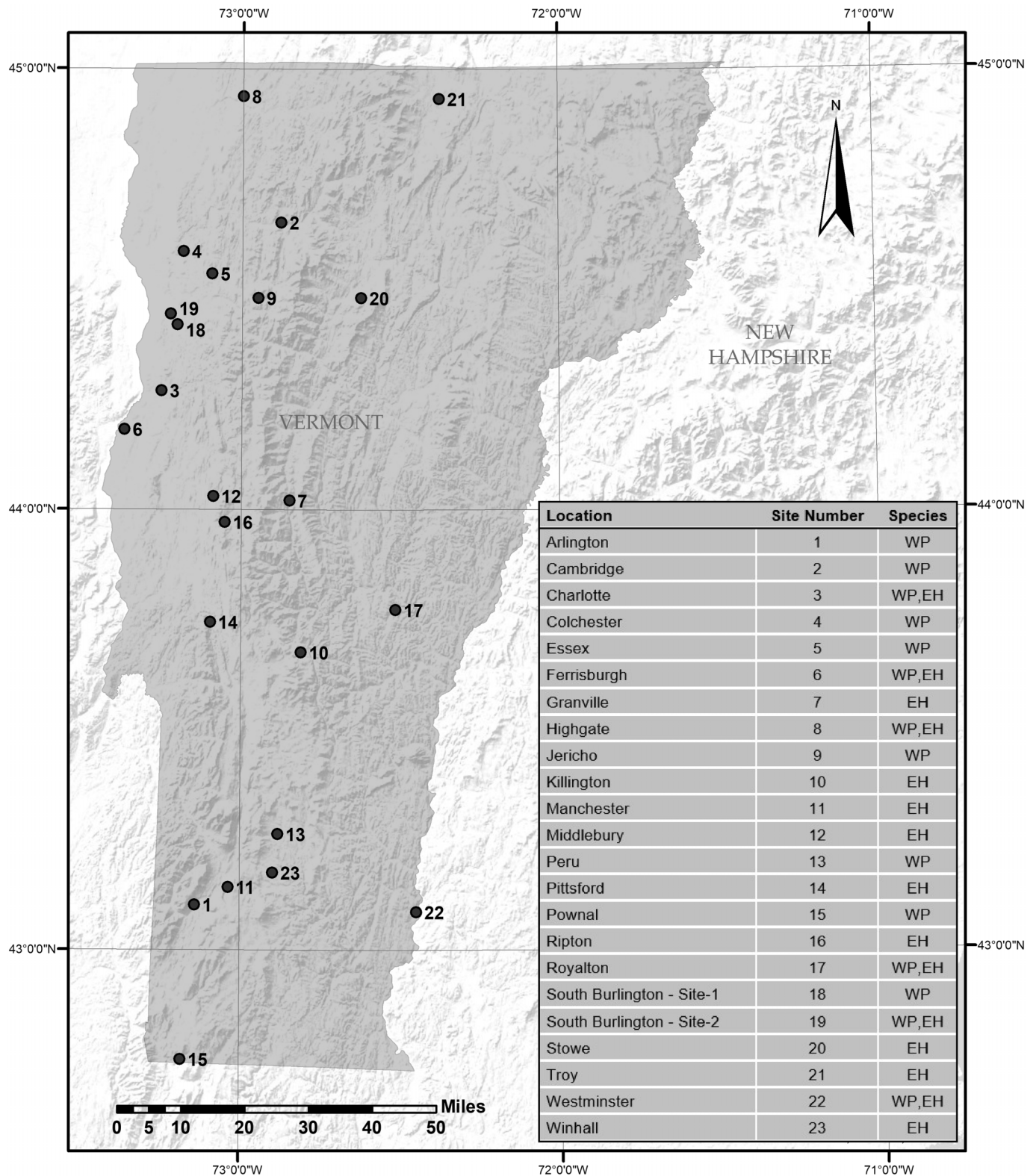
To better isolate potential climate and pollution drivers in these species, we focused on sampling dominant and co-dominant trees, rather than conduct a complete ecological analysis that would include intermediate and suppressed trees. The growth of intermediate and suppressed trees could have a different climate response (Rollinson et al. 2020) and would also include trends such as those related to competition, which, in addition to other factors, could obscure the influence of environmental signals that we were seeking to understand. We extracted increment cores from a total of 476 dominant and co-dominant trees: 219 eastern white pine and 257 eastern hemlock. At each site, between 14 and 24 trees per species were sampled following standard dendrochronological techniques (Stokes and Smiley 1968) by collecting two xylem increment cores per tree at diameter at breast height (DBH: 1.37 m above ground level), perpendicular to the slope and 180° from each other. At site 16 (Fig. 1), only one core per tree was collected. We avoided sampling trees with noticeable bole or crown damage to minimize the influence of non-climatic factors on growth, and to better represent average growth across a site.

Increment core samples were oven-dried, mounted, and sanded with increasingly finer grit sandpaper. Annual tree-ring increments were visually crossdated using the list method (Yamaguchi 1991) and microscopically measured to a 0.001 mm resolution via a Velmex sliding stage unit (Velmex, Inc., Bloomfield, New York) using MeasureJ2X software (v.5.05, VoorTech Consulting, Holderness, New Hampshire). The software program COFECHA (v. 6.06p) was utilized to statistically detect possible crossdating errors (Holmes 1983) and to calculate chronology statistics such as series intercorrelation, average mean sensitivity and autocorrelation (but see Bunn et al. 2013). Individual cores were removed from a site chronology if obvious defects (i.e., knots, insect damage, rot) obscured growth patterns/magnitude resulting in poor correlations with the master chronology. To determine the time period over which all plot chronologies sustained a robust stand-wide signal, expressed population signal (EPS) was computed (R package dplR; Bunn et al. 2016) based on the equation described by Wigley et al. (1984) using a cutoff of 0.80 (but see Buras 2017). When a core's pith was present, we counted tree age at breast height. If pith was not present, we approximated core age with a pith estimator (Speer 2010) using the curvature of the innermost annual rings. We did not assess age for cores that did not exhibit ring sequence curvature, since we were unable to estimate pith in these cases.

Statistical analyses

To establish if any stand-wide release events existed during the chronology period, we analyzed individual tree growth (raw ring width) per plot employing the radial-growth averaging criteria presented by Nowacki and Abrams (1997), using the TRADER package for R (function `growthAveragingALL`; Altman et al. 2014). We

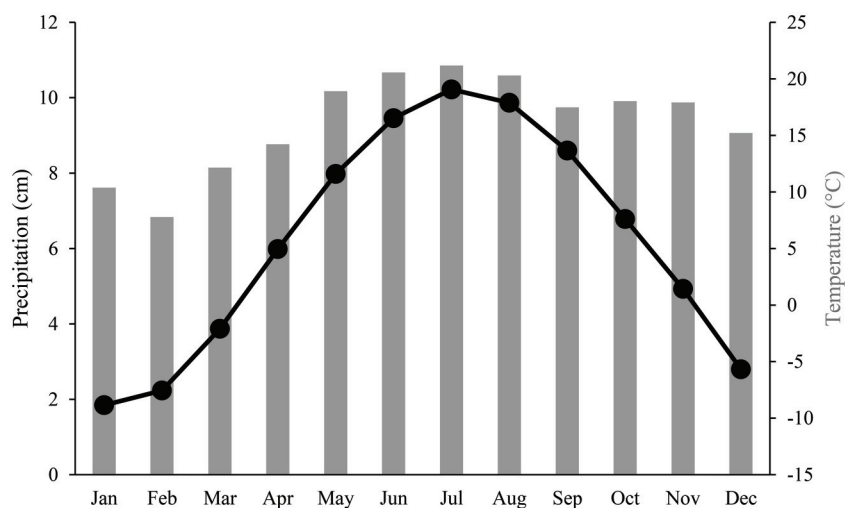
Fig. 1. Locations, plot numbers, and species sampled for the 23 study plots throughout Vermont. WP, eastern white pine; EH, eastern hemlock. Figure was created using ArcGIS 10. Base map courtesy of Esri, USGS, and NOAA.



used a 10-year running median with a 50% threshold to identify major releases for eastern white pine, since it is a fast-growing species of intermediate shade tolerance. Since eastern hemlock is a slow-growing, highly shade tolerant species that can sustain

extended periods of suppression and show dramatic releases when gaps occur in the canopy (Abrams et al. 2001; Black and Abrams 2005), we used a 100% threshold to determine major releases for this species. A stand-wide release was defined as $\geq 25\%$

Fig. 2. Monthly mean temperature (black circles) and monthly total precipitation (grey bars) for the study area from 1940 to 2014 (NOAA National Climatic Data Center 2019).



of trees in the stand experiencing a major release within the same decade (Nowacki and Abrams 1997).

We averaged raw ring width measurements per tree, and standardized growth via two methods. First, we calculated basal area increment (BAI) to assess general growth trends. BAI converts diameter increments (cm/year) into area increments (cm²/year) to reduce size- and age-related growth trends (West 1980). BAI chronologies were created per site and across all sites within a species to generate a study-wide chronology (functions `bai.out` and `chron`, R package `dplR`; Bunn et al. 2016). Second, raw ring widths were standardized using splines, which allow for high frequency endogenous variation (e.g., non-climate related growth resulting from sporadic release events or competition for resources) to be filtered or smoothed from exogenous climate related growth (Cook and Peters 1981). For sites that did not exhibit large release events, we used a 67% *n* cubic smoothing spline with a 50% frequency cutoff. For sites that did exhibit a large release at some point in the chronology, we used the Friedman Super Smoother (Friedman 1984; Pederson et al. 2013) to minimize the effects of disturbance and release, since this method better filtered out non-climatic responses of trees at individual sites. Autoregressive modeling was performed on the standardized series to further lessen the effects of endogenous disturbance, remove the influence of temporal autocorrelation (first order autocorrelations), and enhance the common signal (Cook 1985), which produced prewhitened (residual) chronologies. Mean annual growth values were computed using Tukey's biweight robust mean, which reduces the effect of outliers (Cook and Kairiukstis 1990) and increases the common signal, resulting in a ring width index (RWI). Residual RWI chronologies were created per species for each site and across all sites for each species to create a study-wide chronology. Chronologies were truncated to the common period of 1940–2014, based on EPS results.

Eastern hemlock and eastern white pine were co-occurring at five of our sample sites, enabling us to conduct a direct comparison of growth between these species at the same locations. To test for differences in growth between the species over time (1940–2014), we used an analysis of covariance (ANCOVA) for BAI data for both species at these five sites. Also, per species, sites were then divided into two approximately equal groups based on median tree age (eastern white pine: 95.5 years, eastern hemlock: 136.0 years), mean tree size (DBH; eastern white pine: 60.3 cm, eastern hemlock: 46.5 cm), and site elevation (eastern white pine: 155 m, eastern hemlock: 314 m). We tested stand-level chronologies

for differences in BAI slope (Wilcoxon Rank Sum test) over time based on these characteristics.

Climate data

We evaluated a range of climate parameters for potential associations with radial growth. We averaged climate data from the National Climatic Data Center for the three climate divisions in VT (NOAA National Climatic Data Center 2019), since our study sites spanned these divisions. From this dataset, we selected two direct measures of temperature and two heat indices on which to focus: monthly maximum and minimum temperature (T_{\max} and T_{\min} , respectively), heating degree days (HDD) and cooling degree days (CDD). HDD measures low temperature exposure, calculated as the number of degrees that a day's average temperature is below 18.3 °C (65 °F), while CDD is a gauge of high temperature exposure, calculated as the number of degrees that a day's average temperature is above 18.3 °C (65 °F). While HDD and CDD were formulated to estimate heating and cooling needs within buildings, these indices have been shown to relate to tree growth and physiology and can serve as proxies for aggregated low and high temperature exposures over time (e.g., Kosiba et al. 2018; Stern et al. 2020). For T_{\max} and T_{\min} , we also created seasonal (previous Summer: pJun–pAug; previous Fall: pSep–pNov; Winter: pDec–Feb; Spring: Mar–May; Summer: Jun–Aug; Fall: Sep–Nov) and water year (Wyr: pOct–current Sep) metrics. In addition to obtaining monthly temperature data, we also acquired daily minimum and maximum temperature data to compute Growing Degree Days (GDD), a measure of heat accumulation which may be a better indicator of tree function during the growing season than solely direct measures of temperature. GDD was calculated using the R package `pollen` (function `gdd`; Nowosad 2018).

In addition to temperature data, we utilized the Standardized Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2017) to assess moisture availability. The SPEI takes into account precipitation and potential evapotranspiration, therefore capturing the demand of increased temperatures on moisture availability. Individual site data were averaged to create a state-wide SPEI dataset at the 1-month (SPEI01) and 3-month (SPEI03) time steps. SPEI01 enabled us to identify specific influential months, while SPEI03 allowed us to evaluate relationships on a seasonal basis.

Pollution data

We also acquired pollutant deposition data (NO₃⁻, SO₄²⁻, and rainfall pH) from two National Atmospheric Deposition Program

(National Atmospheric Deposition Program 2017) sites in VT (Bennington and Underhill) and from the Hubbard Brook Ecosystem Study, NH (Likens 2016). Data were averaged for the two VT sites (1982–2014) and regressed against data from NH (1965–2012) to enable us to project the VT data further back in time. Total timespan for this combined dataset was 1965–2014.

Correlations

We calculated moving correlation functions using Pearson's correlations with bootstrap resampling (1000 bootstrap samples; Biondi and Waikul 2004) and a window of 25 years. Correlations were calculated between the RWI chronologies (1940–2014) and monthly, seasonal, and water year climate variables. Monthly correlations spanned a 17-month window from the previous year's June to current year's October to account for lagged and integrated effects of climate. Correlations were considered significant at $P \leq 0.05$ and were conducted using the R package *treeclim* (function *dcc*; Zang and Biondi 2015). We evaluated moving correlations for two reasons: (i) to evaluate the strength of significant stationary correlations over time, and (ii) to test for potential novel associations that occurred for only specific periods of the chronologies but may not be evident in results from long-term static correlations.

In addition to climate data, we conducted moving correlations with pollutant deposition data for the time period with available data (1965–2014). Since the pollutant deposition data exhibited strong decreasing (NO_3^- and SO_4^{2-}) and increasing (pH) trends (supplementary Fig. S1¹), we made the a priori assumption that these trends could lead to spurious correlations with tree growth data. To prevent potential spurious correlations, we calculated first differences of all pollutant deposition variables, as well as tree growth for both species, and then conducted the correlations. Correlations were calculated between RWI and annual totals for Wyr pollution deposition variables. A window of 10 years was used for these moving correlations to better assess any potential responses to recent changes in pollution deposition.

Results

Chronology statistics and BAI growth trends

Eastern white pine and eastern hemlock exhibited similar chronology statistics (Table 1). Eastern white pine had an estimated median site age range of 76.0 to 200.5 years, and eastern hemlock showed a range of 55.5 to 190.5 years (supplementary Tables S1 and S2¹). The mean DBH range was 49.0–87.9 cm for eastern white pine sites and 35.9–58.3 cm for eastern hemlock sites (supplementary Tables S1 and S2¹).

BAI growth for both species increased throughout their chronologies (Fig. 3). Maximum growth was 40.7 cm² in 2012 for eastern white pine and 26.2 cm² in 2010 for eastern hemlock. For eastern white pine, there were no differences in BAI slopes over time for stand-level chronologies between elevation and size groups. Eastern white pine sites in the younger age group category grew at a significantly faster rate throughout the chronology than older sites (Wilcoxon Rank Sum test; $Z = 0.04$, $P \leq 0.05$). Eastern hemlock showed no differences in BAI slope over time for stand-level chronologies in terms of elevation, size, or age groupings. Results from the ANCOVA test, which compared growth trajectories of the two species, showed that throughout the chronology and across all sites, eastern white pine has been growing at a faster rate than eastern hemlock ($F_{[1,2063]} = 189.49$, $P \leq 0.0001$). To ensure that this difference in growth was not due to variations in site conditions that could have been confounded with species, we also compared growth specifically at the five sites where the two species co-occurred. Even with a reduced sample size for comparison, eastern white pine had greater growth

Table 1. Summary of regional chronology statistics for the two study species — eastern white pine and eastern hemlock.

Statistic	Eastern white pine	Eastern hemlock
<i>n</i> sites	13	15
<i>n</i> trees	219	257
<i>n</i> cores	449	492
Longest chronology span	1794–2015	1735–2015
Interseries correlation	0.65	0.62
Mean sensitivity	0.24	0.26
First-order autocorrelation	0.78	0.78
Mean correlation between trees	0.52	0.43
Expressed population signal	0.90	0.89
Signal-to-noise ratio	13.2	12.0

Note: Statistics shown are average values for all sites within a species from ring-width index chronologies. For individual site statistics, see supplementary Tables S1 and S2¹.

than eastern hemlock at these sites ($F_{[1,744]} = 260.42$, $P \leq 0.0001$). Seven sites showed evidence of growth releases of unknown origin during the chronology timespan (supplementary Table S3¹).

Climate- and pollutant-growth correlations

Eastern white pine

Eastern white pine exhibited sustained significant positive correlations with spring and summer moisture throughout its chronology (Fig. 4). This was evident in individual months as May, June, and July SPEI01 (r values ranging from 0.31 to 0.72, $P \leq 0.05$) and seasonal metrics with May, June, July, and August SPEI03 (r values ranging from 0.33 to 0.80, $P \leq 0.05$). July SPEI03, an index of available moisture for May, June, and July, showed the most consistent significant correlations and also the strongest correlation coefficients of all moisture and temperature variables for this species for the entirety of the chronology period ($r = 0.80$, $P \leq 0.05$; Fig. 4). During the last 40 years only, the eastern white pine chronology showed negative associations with previous summer SPEI03 metrics (previous June and July; r values ranging from -0.59 to -0.34 , $P \leq 0.05$; supplementary Fig. S2¹).

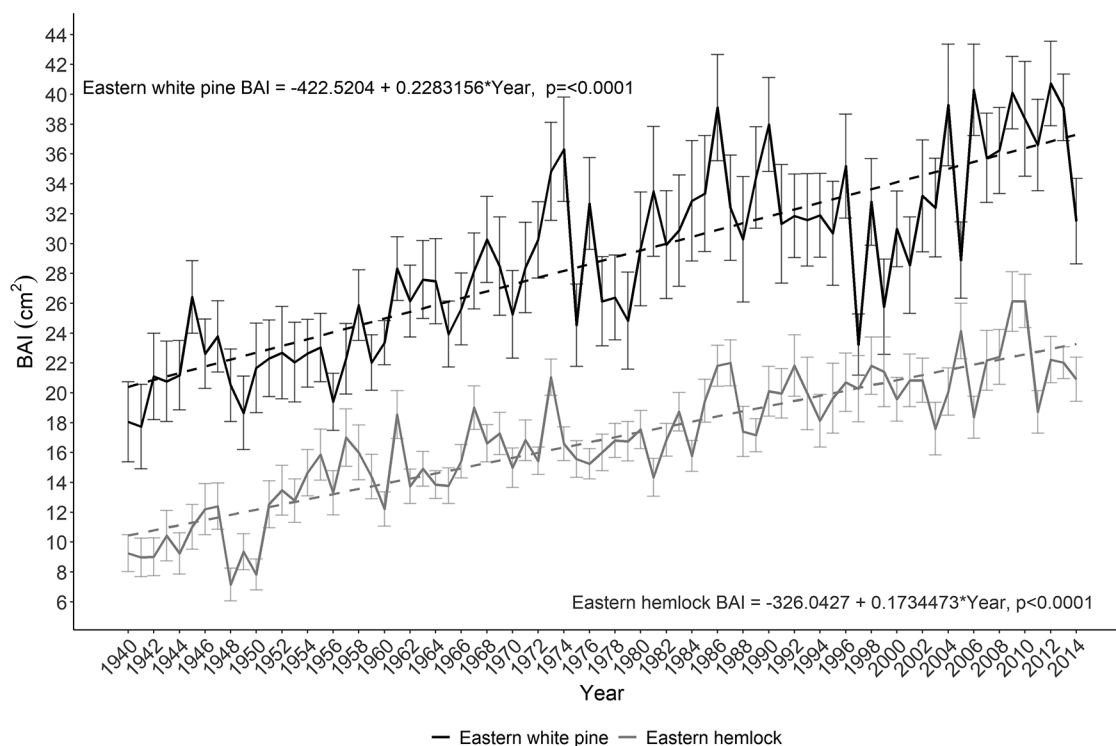
Correlations between eastern white pine growth and temperature showed both positive and negative associations depending on the season. Correlations with pDec T_{\max} switched from positive to negative over the length of the chronology and were negative for the majority of the last 50 years (r values ranging from -0.56 to 0.44, $P \leq 0.05$; supplementary Fig. S3¹). March T_{\max} (r values ranging from 0.28 to 0.48, $P \leq 0.05$) showed a positive association during the last 40 years of the chronology, along with March GDD since the 1970s (r values ranging from 0.32 to 0.56, $P \leq 0.05$; Fig. 5). In contrast to spring months, eastern white pine growth showed a negative correlation with June T_{\max} (r values ranging from -0.74 to -0.45 , $P \leq 0.05$) during the past 40 years and summer T_{\max} (r values ranging from -0.58 to -0.21 , $P \leq 0.05$; Fig. 5) during the past 50 years. Eastern white pine growth showed consistent positive associations with pJuly T_{\max} starting in the 1960s (r values ranging from 0.35 to 0.52, $P \leq 0.05$; supplementary Fig. S3¹). This pattern was also evident in pJuly GDD, which switched from a negative to positive correlation over time (r values ranging from -0.44 to 0.51, $P \leq 0.05$; supplementary Fig. S3¹). No significant patterns were found in correlations between eastern white pine growth and the three Wyr pollution metrics.

Eastern hemlock

Eastern hemlock showed a consistent significant correlation with June SPEI01 until the last 40 years (r values ranging from

¹Supplementary data are available with the article at <https://doi.org/10.1139/cjfr-2020-0512>.

Fig. 3. Mean basal area increment (BAI) growth (\pm SE) from 1940 to 2014 for eastern white pine (black line) and eastern hemlock (grey line), along with linear regression of growth over time (dashed lines and associated equations).



0.26 to 0.47, $P \leq 0.05$; Fig. 6). Similarly, June, July, and August SPEI03 were significant only during the first decades of the chronology (r values ranging from 0.34 to 0.59, $P \leq 0.05$; Fig. 6 and supplementary Fig. S4¹). pAugust SPEI01 (r values ranging from 0.40 to 0.63, $P \leq 0.05$) and pSep SPEI03 (r values ranging from 0.28 to 0.66, $P \leq 0.05$) were also significant, but only during the last 40 years (supplementary Fig. S4¹).

Eastern hemlock showed a negative association with pJuly T_{\max} (r values ranging from -0.51 to -0.41 , $P \leq 0.05$), and was also seen as positive correlations with pJuly HDD (a measure of cold; r values ranging from 0.31 to 0.59, $P \leq 0.05$; supplementary Fig. S5¹). The species also exhibited a positive association with warmer previous fall temperatures: pOctober T_{\max} (r values ranging from 0.42 to 0.57, $P \leq 0.05$) and pOct HDD (r values ranging from -0.54 to -0.50 , $P \leq 0.05$; Fig. 7). Feb GDD exhibited a changing pattern through time: while eastern hemlock growth showed a positive correlation with Feb GDD at the beginning of its chronology (r values ranging from 0.30 to 0.35, $P \leq 0.05$), it showed a negative correlation more recently (r values ranging from -0.54 to -0.34 , $P \leq 0.05$; supplementary Fig. S5¹). A positive association was seen between eastern hemlock growth and March T_{\min} (r values ranging from 0.43 to 0.54, $P \leq 0.05$), but only during the first 30 years of the chronology, which then disappeared (Fig. 7). Similarly, associations with May T_{\max} (r values ranging from -0.58 to -0.40 , $P \leq 0.05$; Fig. 7) and May HDD (r values ranging from 0.35 to 0.57, $P \leq 0.05$; supplementary Fig. S5¹) were significant only early in the chronology. Eastern hemlock did not exhibit any significant patterns with Wyr pollution metrics (1965–2014).

Discussion

General growth patterns

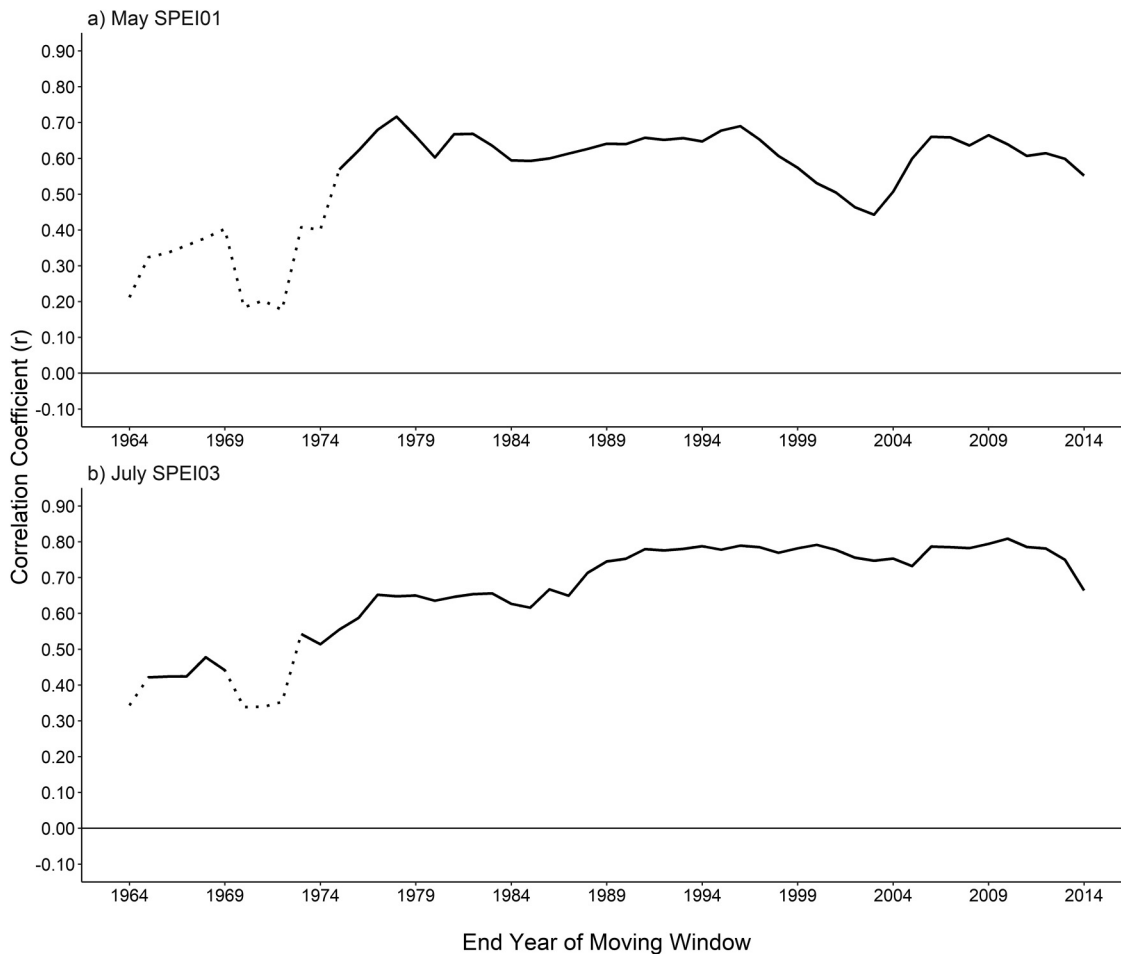
Both eastern white pine and eastern hemlock exhibited increasing growth, with the highest levels occurring in the most recent decades. Overall, eastern white pine showed greater maximum growth than eastern hemlock, and a higher rate of growth throughout the chronology (1940–2014). These trends are consistent with

each species' ecological niche and known silvics. For example, eastern white pine is intermediate in shade tolerance and has a remarkable potential growth rate compared to other coniferous and hardwood species within its range, whereas eastern hemlock is the most shade tolerant of all North American species and has a relatively low growth potential (Burns and Honkala 1990).

Correlations with moisture

For eastern white pine, spring and summer moisture availability maintained a strong association with growth throughout the species' chronology. This suggests that even though precipitation has been increasing in the region during the past several decades (Janowiak et al. 2018), moisture is still limiting growth to some degree. Summer moisture may actually be more limiting to eastern white pine growth in recent years than it has been in the past; the ten strongest correlations with summer moisture emerged during the last 21 years of the chronology (highest r values for July SPEI03 ranging from 0.78 to 0.80, $P \leq 0.01$). This counterintuitive finding of more apparent sensitivity to moisture during a period of increased precipitation (supplementary Fig. S6¹) may reflect the greater periodicity and intensity of precipitation (i.e., variability) in recent years — a combination that can result in greater runoff, reduced soil infiltration and longer gaps between rain events (Janowiak et al. 2018). This trend of limited tree growth potentially due to variability in precipitation has been found in deciduous tree growth in the northeastern US (Martin-Benito and Pederson 2015). Longer gaps between precipitation events can create mini-drought conditions, and drought sensitivity has been observed for 24 tree species in eastern North America (D'Orangeville et al. 2018). Moreover, in pine ecosystems, water stress has been shown to be a considerable determinant in reducing photosynthetic rates (Teskey et al. 1994). Positive relationships between eastern white pine growth and moisture availability in May through August have also been observed in multiple other studies (Cook and Jacoby 1977; Abrams et al. 2000; Kipfmüller et al. 2010; Chhin et al. 2013). Our finding of eastern white pine's

Fig. 4. Moving correlations of standardized radial growth of white pine with (a) May SPEI01 and (b) July SPEI03, two of the spring and summer moisture metrics that exhibited sustained significance through the majority of the white pine growth chronology. Dotted lines represent a non-significant relationship and solid lines a significant relationship at $P \leq 0.05$. Year designations represent the last year of a 25-year moving window.



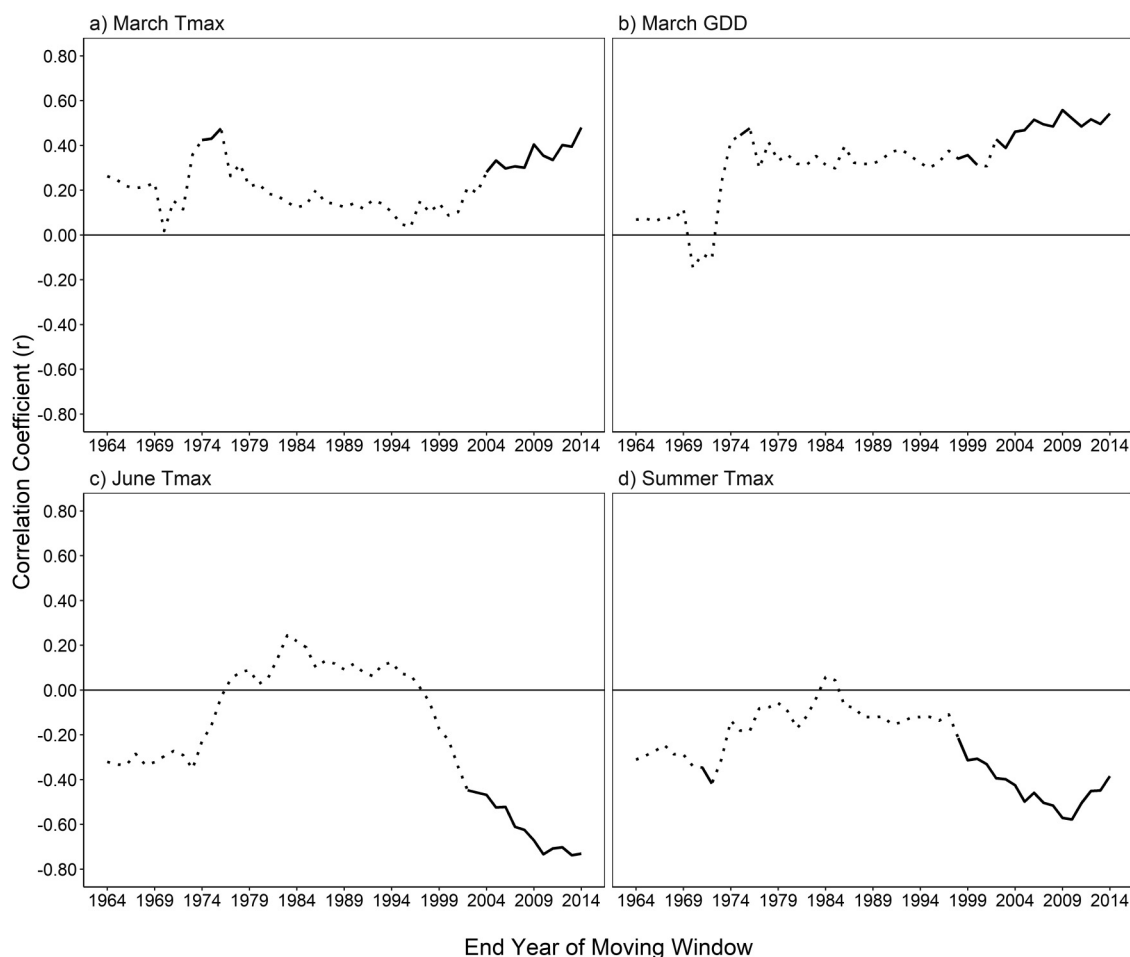
increased sensitivity to moisture in recent decades despite generally increased precipitation levels may highlight the limitations of broad generalized climate data (e.g., a moisture index for an entire month), relative to potentially more ecologically relevant metrics such as those designed to capture extreme climate events (e.g., Oswald et al. 2018).

In addition to positive associations with current year moisture availability, eastern white pine showed negative associations with previous year's moisture availability, which only became dominant during the last 40 years of the chronology (supplementary Fig. S2¹). One possible explanation for this relationship is eastern white pine needle damage, a disease complex that causes yellowing and early needle-drop (Vermont Department of Forests Parks and Recreation 2020). Previous year's spring and summer precipitation has been found to be a predictor of eastern white pine needle damage in northern New England, with higher precipitation levels being associated with greater fungal damage to and mortality of needles (Wyka et al. 2017). Consistent with these findings, our eastern white pine sites exhibited negative correlations with pJune and pJuly SPEI03 (supplementary Fig. S2¹), which are indicative of moisture regimes for the spring and summer seasons.

Our eastern hemlock findings indicated a significant positive association with current summer moisture that has faded in the last 40 years, but those positive correlations with previous

summer and fall moisture have emerged only during the last 40 years. Similar to our findings of a disappearing association with current-year moisture in recent decades, Bigelow et al. (2019) observed that for the period of 1978–2011, eastern hemlock growth showed only a weak relationship to current year precipitation variables in New York state, which may be slightly different due to its more inland location. Other studies have observed positive correlations between eastern hemlock radial growth and both current and previous summer moisture availability in eastern North America (Cook and Jacoby 1977; Cook and Cole 1991; Abrams et al. 2000; Tardif et al. 2001; Black and Abrams 2005), although these studies utilized static correlations rather than moving correlations, and looked at different or longer time periods. Using moving correlations, Saladyga and Maxwell (2015) found consistent positive correlations between eastern hemlock growth (1896–2012) and June precipitation in the Central Appalachian region. A positive correlation between eastern hemlock growth and pSeptember precipitation was also found for an eastern hemlock site in New York (D'Arrigo et al. 2001), as we did with pSeptember SPEI03. The apparent change in the timing and influence of moisture on eastern hemlock growth in the northern forest may reflect a shift in the region's moisture regime: the region experienced both overall drier conditions and a major drought (1964–1967; NOAA National Centers for Environmental Information 2018) during the first half of the chronology, while in contrast, the

Fig. 5. Moving correlations of standardized radial growth of white pine with numerous temperature variables: (a) March T_{\max} , (b) March growing degree days (GDD), (c) June T_{\max} , and (d) Summer T_{\max} . Dotted lines represent a non-significant relationship and solid lines a significant relationship at $P \leq 0.05$. Year designations represent the last year of a 25-year moving window.



region has experienced unusually high levels of precipitation during the second half of the chronology (Pederson et al. 2013).

Correlations with temperature across the seasons

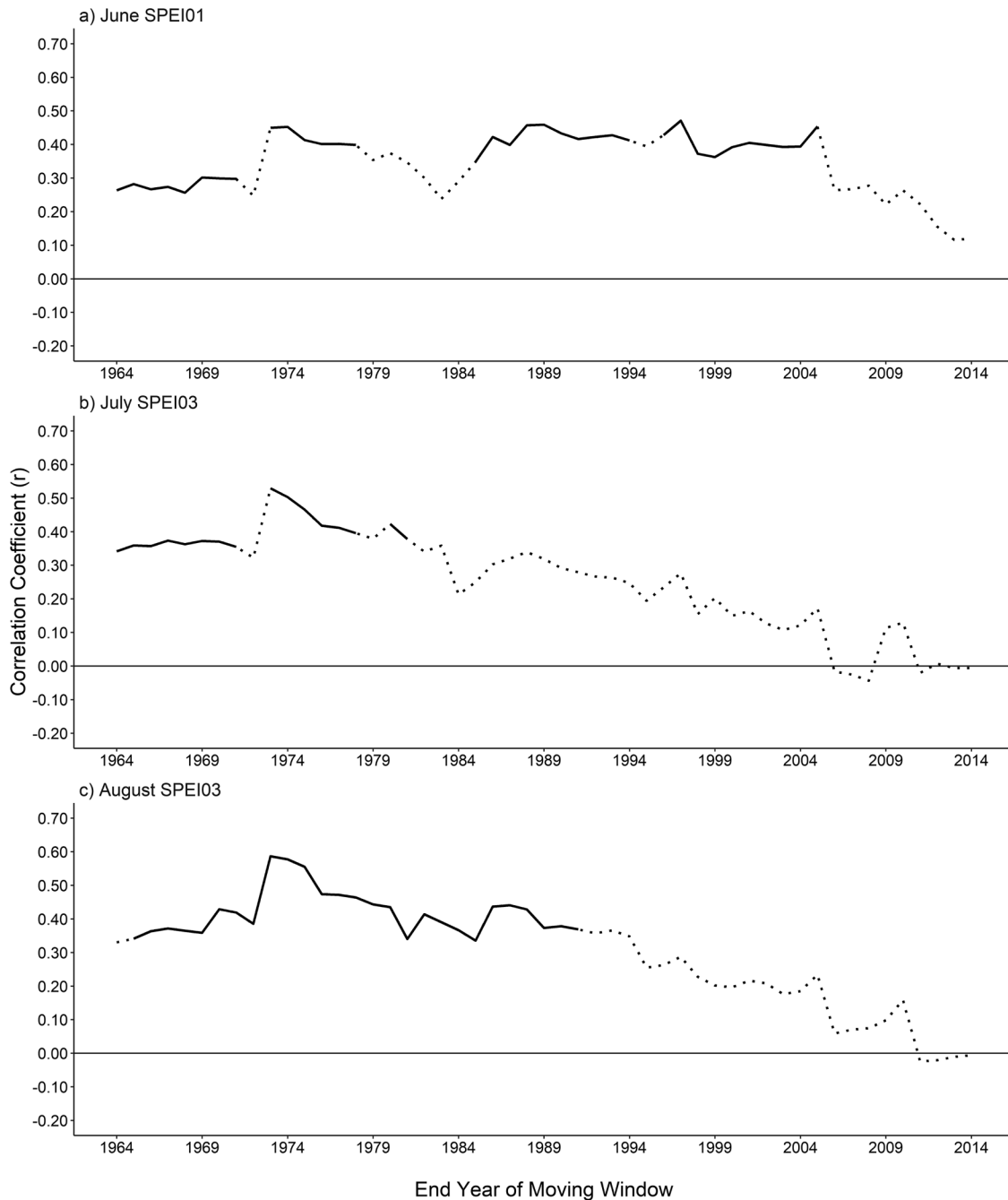
Spring

Both species showed positive associations with variables signifying warmer spring temperatures, although these associations appeared to be quite transitory, especially for eastern hemlock (Figs. 5 and 7). This latter finding is somewhat surprising because numerous studies have observed a positive association between growth and March temperatures for eastern hemlock across a wide spatial range in eastern North America, though these studies utilized static correlations (Cook and Cole 1991; Abrams et al. 2001; Tardif et al. 2001; Saladyga and Maxwell 2015). Similar to our study, in examining moving correlations, Saladyga and Maxwell (2015) found a positive correlation between eastern hemlock growth and average March temperatures that disappeared around 1970. It has been suggested that early spring temperatures can melt snow, enabling soils to warm and photosynthesis to resume (Cook and Cole 1991). Indeed, Hadley and Schedlbauer (2002) observed a rapid increase in C uptake by eastern hemlock trees in mid-April in Massachusetts, as well as continued photosynthesis in October and November. C storage in their study was regulated more by T_{\min} than soil temperature, suggesting that decreasing frosts in spring and fall as a

result of climate change could promote greater C storage in eastern hemlock stands. We found that positive relationships between growth and fall temperatures faded over time, whereas those with spring temperatures were persistent, suggesting that temperature trends for spring may ultimately be more consequential. In a subsequent study, Hadley et al. (2008) found that eastern hemlock forests stored more C throughout the course of a relatively warm year than a compatriot deciduous species, red oak. This finding underscores the possibility that warmer fall, winter and spring seasons could increase the C storage capabilities of some coniferous mid-latitude forests, unless significant increases in summer temperatures lead to net C losses (Hadley et al. 2008).

Previous studies on eastern white pine have shown links between photosynthesis and spring temperatures. McGregor and Kramer (1963) found the average rate of photosynthesis in North Carolina in eastern white pine seedlings peaked in April. In Michigan, Jurik et al. (1988) observed a positive relationship between April temperatures and eastern white pine carbon dioxide exchange rates. In their study, soil temperatures were the best predictor of maximum C exchange because warmer soils allowed for increased root conductance followed by stomatal conductance (Jurik et al. 1988). Our findings are consistent with their evidence that a sustained period of warmer spring air temperatures may support greater photosynthesis (Jurik et al. 1988) and growth. This may be particularly true for eastern white

Fig. 6. Moving correlations of standardized radial growth of eastern hemlock with (a) June SPEI01, (b) July SPEI03, and (c) August SPEI03. Dotted lines represent a non-significant relationship and solid lines a significant relationship at $P \leq 0.05$. Year designations represent the last year of a 25-year moving window. For further explanations of moisture variables see Methods.



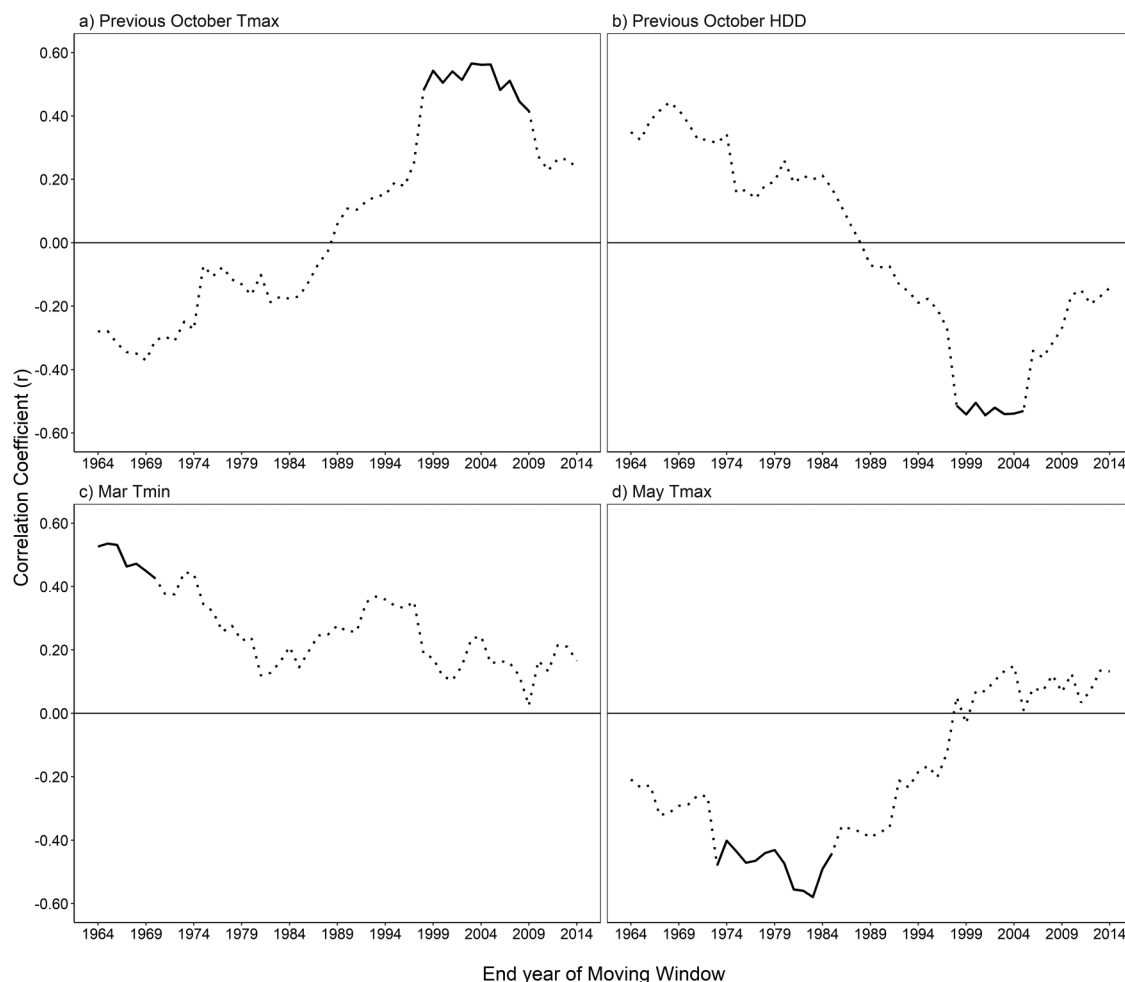
pine, since positive correlations with warmer March months were consistently and increasingly evident in our study over the past four decades (Fig. 5).

Summer

The growth of eastern white pine and to a lesser extent eastern hemlock was negatively correlated with summer temperatures. For eastern white pine, these associations were particularly true in the most recent decades; the strongest correlation with temperature for eastern white pine was with June T_{\max} during the window of 1989–2013 ($r = -0.74$, $P \leq 0.05$). In our study area, June T_{\max} has been increasing (supplementary Fig. S6¹). A negative

relationship between eastern white pine growth and summer temperatures has been found in other locations throughout the species' range (Cook and Jacoby 1977; Kipfmüller et al. 2010; Chhin et al. 2013). Along with our findings, these studies point towards heat stress and heat-induced moisture limitations. Eastern hemlock exhibited negative correlations with higher previous summer temperatures (supplementary Fig. S5¹) — a pattern that has also been observed across a wide range of eastern hemlock stands (Cook and Cole 1991; D'Arrigo et al. 2001; Tardif et al. 2001). Negative associations between temperature and growth often reflect the influence of heat-induced moisture limitations (Rennenberg et al. 2006). However, the persistence of these

Fig. 7. Moving correlations of standardized radial growth of eastern hemlock with multiple temperature variables: (a) pOctober T_{\max} , (b) pOctober heating degree days (HDD), (c) March T_{\min} , and (d) May T_{\max} . Dotted lines represent a non-significant relationship and solid lines a significant relationship at $P \leq 0.05$. Year designations represent the last year of a 25-year moving window. For further explanations of temperature variables see Methods.



associations into the recent pluvial (e.g., when negative relations between growth and moisture have diminished for eastern hemlock) may suggest that direct heat stress is also becoming more important.

Autumn

In recent decades, eastern hemlock growth was positively associated with pOctober T_{\max} (Fig. 7), a pattern also observed in Pennsylvania as a correlation with average October temperatures (Black and Abrams 2005). On clear, mild days, temperate conifers can exhibit fall photosynthetic rates comparable with summer rates, so long as needles do not freeze (Havranek and Tranquillini 1995). Whatever the physiological causes and possible adaptive consequences, it appears that relationships between eastern hemlock growth and temperature during autumn are in flux.

Winter

Since minimum winter temperatures have been increasing more than temperatures in any other season (Janowiak et al. 2018), one might expect to find evidence that eastern white pine and eastern hemlock can capitalize on an ability to photosynthesize during winter, too. Indeed, in recent decades only, eastern hemlock exhibited positive correlations with warmer February temperatures (supplementary Fig. S5¹). Eastern white pine exhibited

negative growth with warmer pDecember months during the past 45 years (supplementary Fig. S3¹). Jurik et al. (1988) described that for eastern white pine, even multiple days with warm winter air temperatures may not increase soil temperatures enough to enable a resumption of the species' full photosynthetic capacity. If temperatures rise but needles have a limited photosynthetic capacity, warmed foliage will experience increases in respiration that deplete non-structural C reserves (e.g., Ögren et al. 1997) that otherwise could fuel woody growth in spring.

Changing associations over time

In looking at changes in climate associations over time, one notable feature is that certain significant spring and summer temperature-growth correlations for eastern hemlock have shown few consistent patterns (Fig. 7, supplementary Fig. S5¹). This contrasts with eastern white pine, which showed a strengthened association with spring and summer temperatures in later decades (Fig. 5). This suggests that spring and summer temperatures may be important controlling factors that influence growth for eastern white pine, but that other factors are now more important modulators of eastern hemlock growth.

Pollution deposition-growth correlations

Neither species showed significant associations between growth and any pollutant metric. This was not unexpected because these

particular temperate conifers have not been identified as being particularly vulnerable to damage by acid deposition (e.g., Schaberg et al. 2001, 2010). This is in stark contrast to red spruce, which is probably the best documented example of pollution-associated tree decline in North America (e.g., DeHayes et al. 1999; Driscoll et al. 2001; Kosiba et al. 2018). Nonetheless, the lack of any relationships between growth and pollution metrics were somewhat surprising in that through broad-scale forest inventories, both species showed negative associations between N and (or) S deposition and growth (Horn et al. 2018). However, because Horn et al. (2018) did not compare growth to the first differences of pollutant deposition variables, these associations may partially reflect simultaneous but independent patterns of increased growth and decreased pollution inputs.

Tradeoffs in response — implications for the growth of temperate conifers

An organizing premise of this study was to assess if temperate conifers other than red spruce might be experiencing enhanced growth associated with milder shoulder seasons and a functional lengthening of the growing season. Our findings of positive associations between eastern white pine growth and warmer spring temperatures, particularly in recent decades, are consistent with this premise. At the beginning of its chronology, eastern hemlock also showed positive associations between temperature and growth in spring, though unlike eastern white pine, this was also evident in early autumn. Associations between increased growth and higher spring (eastern white pine and eastern hemlock), autumn and even winter temperatures (eastern hemlock) are consistent with patterns documented for red spruce (Kosiba et al. 2018) and support the hypothesis that temperate conifer growth may benefit from temperature increases outside of the traditional growing season (though changing relationships for eastern white pine in winter raise questions about the influences for this species and season). However, negative associations between growth and summer temperatures for all three temperate conifers (here and Kosiba et al. 2018), indicate that overall warming will likely involve tradeoffs between positive (non-growing season) and negative (growing season) impacts. Furthermore, growth can be further modulated by the positive influence of adequate moisture in eastern white pine (here), red spruce (Kosiba et al. 2018), and possibly other temperate conifers as well. Thus, the net impact of changes in temperature and moisture regimes will depend on how these influences combine or possibly interact through time. For example, a future with hotter and drier summers (Janowiak et al. 2018) could reduce C storage and offset growth gains associated with the milder shoulder seasons (Hadley and Schedlbauer 2002). This is especially important to consider since the northeast region of the US is projected to experience a greater increase in temperature than other parts of the country (US Global Change Research Program 2018). The recent high growth of eastern white pine and eastern hemlock (here) and red spruce (Kosiba et al. 2018) suggest that any tradeoffs in climate and pollution response currently result in a net positive influence on growth. However, additional study of growth-climate relationships for temperate conifers across broader temperature and moisture gradients are needed to better understand the overall trend in C gain potential of this tree group as environmental change continues. Additionally, this study focuses on the growth of existing canopy trees and does not extend to potential C capture of future regenerations.

Our evidence of historically increasing eastern white pine and eastern hemlock growth (Fig. 3) is in line with future predictions for VT from the Climate Change Tree Atlas (Prasad et al. 2007—ongoing). Based on importance values (dominance of a species in a given forest area), projections from the Tree Atlas show that eastern white pine and eastern hemlock are projected to decrease slightly at lower elevations and increase at higher elevations and latitudes within VT. One of the top predictors of suitable habitat

for eastern white pine and eastern hemlock in the Tree Atlas is mean July temperature, which highlights the role that warmer summer temperatures could play in altering the future habitat suitability for these species (Prasad et al. 2007—ongoing). However, potential increases in growth related to warmer springs (eastern white pine) and autumn (eastern hemlock) could offset the negative influences of hot summer temperatures. Indeed, it would be informative to integrate our findings of the positive associations of higher shoulder season temperatures to existing models of future habitat suitability to refine projections for temperate conifers in the region.

Data availability statement

The datasets generated for this study are available for download from The DendroEcological Network at <https://www.uvm.edu/femc/dendro#data>.

Acknowledgements

We thank Jennifer Pontius and Anthony D'Amato for thoughtful suggestions regarding manuscript edits. We also thank Charles Cogbill, Alexandra Kosiba, and Aiko Weverka for help in the field, and Rebecca Rossell, Isabel Molina, Jeremy Gerber, Elizabeth Bannar, and Jack Kilbride for their assistance in the field and laboratory. This research was supported by the USDA Forest Service and the USDA McIntire-Stennis Forest Research Program. In addition, we thank personnel from the Green Mountain National Forest, the Vermont Department of Forests, Parks and Recreation, the Ethan Allen Firing Range, the towns of Essex and South Burlington, and Rose Paul at The Nature Conservancy of Vermont for access to field sites.

References

- Abrams, M.D. 2001. Eastern white pine versatility in the presettlement forest. *Bioscience*, **51**(11): 967–979. doi:10.1641/0006-3568(2001)051[0967:EWPVIT]2.0.CO;2.
- Abrams, M.D., Gevel, S.V.D., Dodson, R.C., and Copenheaver, C.A. 2000. The dendroecology and climatic impacts for old-growth white pine and hemlock on the extreme slopes of the Berkshire Hills, Massachusetts, U.S.A. *Can. J. Bot.* **78**(7): 851–861. doi:10.1139/b00-057.
- Abrams, M.D., Copenheaver, C.A., Black, B.A., and Gevel, S.V.D. 2001. Dendroecology and climatic impacts for a relict, old-growth, bog forest in the Ridge and Valley Province of central Pennsylvania, USA. *Can. J. Bot.* **79**(1): 58–69. doi:10.1139/b00-145.
- Altman, J., Fibich, P., Dolezal, J., and Aakala, T. 2014. TRADER: A package for Tree Ring Analysis of Disturbance Events in R. *Dendrochronologia*, **32**(2): 107–112. doi:10.1016/j.dendro.2014.01.004.
- Bigelow, S.W., Runkle, J.R., and Oswald, E.M. 2019. Competition, climate, and size effects on radial growth in an old, growth hemlock forest. *Forests*, **11**(1): 52. doi:10.3390/f11010052.
- Biondi, F., and Waikul, K. 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Comput. Geosci.* **30**(3): 303–311. doi:10.1016/j.cageo.2003.11.004.
- Black, B.A., and Abrams, M.D. 2005. disturbance history and climate response in an old-growth hemlock-white pine forest, Central Pennsylvania. *J. Torrey Bot. Soc.* **132**(1): 103–114. doi:10.3159/1095-5674(2005)132[103:DHACRI]2.0.CO;2.
- Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., and Zang, C. 2016. dplR: Dendrochronology Program Library in R. R package version 1.6.4. Available from <http://CRAN.R-project.org/package=dplR>.
- Bunn, A.G., Jansma, E., Korpela, M., Westfall, R.D., and Baldwin, J. 2013. Using simulations and data to evaluate mean sensitivity (̄) as a useful statistic in dendrochronology. *Dendrochronologia*, **31**(3): 250–254. doi:10.1016/j.dendro.2013.01.004.
- Buras, A. 2017. A comment on the expressed population signal. *Dendrochronologia*, **44**: 130–132. doi:10.1016/j.dendro.2017.03.005.
- Burns, R.M., and Honkala, B.H. 1990. *Silvics of North America. Agriculture handbook 654*. United States Department of Agriculture, Washington, DC.
- Chhin, S., Chumack, K., Dahl, T., David, E.T., Kurzeja, P., Magruder, M., and Telewski, F.W. 2013. Growth-climate relationships of *Pinus strobus* in the floodway versus terrace forest along the banks of the Red Cedar River, Michigan. *Tree-ring Res.* **69**(2): 37–47. doi:10.3959/1536-1098-69.2.37.
- Cogbill, C.V. 2000. Vegetation of the presettlement forests of northern New England and New York. *Rhodora*, **102**: 250–276.
- Cook, E.R. 1985. A time series analysis approach to tree ring standardization (dendrochronology, forestry, dendroclimatology, autoregressive process).

- Ph.D. Dissertation, School of Renewable Natural Resources, The University of Arizona, Tucson, AZ.
- Cook, E.R., and Cole, J. 1991. On predicting the response of forests in eastern North America to future climatic change. *Clim. Change*. **19**(3): 271–282. doi:10.1007/BF00140166.
- Cook, E.R., and Jacoby, G.C. 1977. Tree-ring-drought relationships in the Hudson Valley, New York. *Science*. **198**: 399–401. doi:10.1126/science.198.4315.399. PMID:17809441.
- Cook, E.R., and Kairiukstis, L.A. 1990. *Methods of Dendrochronology*. Kluwer Academic Publishers, Boston.
- Cook, E.R., and Peters, K. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-ring Bull.* Available from <https://repository.arizona.edu/handle/10150/261038> [accessed 6 August 2018].
- D'Arrigo, R.D., Schuster, W.S.F., Lawrence, D.M., Cook, E.R., Wiljanen, M., and Thetford, R.D. 2001. Climate-growth relationships of eastern hemlock and chestnut oak from black rock forest in the highlands of south-eastern New York. *Tree-ring Res.* **57**(2): 183–190. Available from <http://hdl.handle.net/10150/251622>.
- DeHayes, D.H., Schaberg, P.G., Hawley, G.J., and Strimbeck, G.R. 1999. Acid rain impacts on calcium nutrition and forest health: alteration of membrane-associated calcium leads to membrane destabilization and foliar injury in red spruce. *Bioscience*, **49**(10): 789–800. doi:10.2307/1313570.
- D'Orangeville, L., Maxwell, J., Kneeshaw, D., Pederson, N., Duchesne, L., Logan, T., et al. 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. *Glob. Change Biol.* **24**(6): 2339–2351. doi:10.1111/gcb.14096.
- Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., et al. 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. *Bioscience*, **51**(3): 180–198. doi:10.1641/0006-3568(2001)051[0180:ADITNU]2.0.CO;2.
- Ellison, A.M. 2014. Experiments are revealing a foundation species: a case study of eastern hemlock (*Tsuga canadensis*). *Adv. Ecol.* **2014**: 11. doi:10.1155/2014/456904.
- Ellison, A.M., Orwig, D.A., Fitzpatrick, M.C., and Preisser, E.L. 2018. The past, present, and future of the hemlock woolly adelgid (*Adelges tsugae*) and its ecological interactions with eastern hemlock (*Tsuga canadensis*) forests. *Insects*, **9**(4): 172. Available from <https://www.mdpi.com/2075-4450/9/4/172>. doi:10.3390/insects9040172.
- Eschtruth, A.K., Evans, R.A., and Battles, J.J. 2013. Patterns and predictors of survival in *Tsuga canadensis* populations infested by the exotic pest *Adelges tsugae*: 20 years of monitoring. *For. Ecol. Manage.* **305**: 195–203. doi:10.1016/j.foreco.2013.05.047.
- Foster, D.R., D'Amato, A., Baiser, B., Ellison, A.M., and Plotkin, A.B. 2014. *Hemlock: a forest giant on the edge*. Yale University Press.
- Friedman, J.H. 1984. *A variable span smoother*. Stanford University, Lab for Computational Statistics, Stanford, California, USA. Available from <https://www.siac.stanford.edu/pubs/siacpubs/3250/siac-pub-3477.pdf>.
- Hadley, J.L. 2000. Effect of daily minimum temperature on photosynthesis in eastern hemlock (*Tsuga canadensis* L.) in autumn and winter. *Arct. Antarct. Alp. Res.* **32**(4): 368–374. doi:10.1080/15230430.2000.12003379.
- Hadley, J.L., and Schedlbauer, J.L. 2002. Carbon exchange of an old-growth eastern hemlock (*Tsuga canadensis*) forest in central New England. *Tree Physiol.* **22**(15–16): 1079–1092. doi:10.1093/treephys/22.15-16.1079. PMID:12414368.
- Hadley, J.L., Kuzeja, P.S., Daley, M.J., Phillips, N.G., Mulcahy, T., and Singh, S. 2008. Water use and carbon exchange of red oak and eastern hemlock-dominated forests in the northeastern USA: implications for ecosystem-level effects of hemlock woolly adelgid. *Tree Physiol.* **28**(4): 615–627. doi:10.1093/treephys/28.4.615. PMID:18244947.
- Havranek, W.M., and Tranquillini, W. 1995. Physiological processes during winter dormancy and their ecological significance. In *Ecophysiology of coniferous forests*. Edited by W. Smith and T. Hinkley. Academic Press, New York. pp. 95–124.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bull.* **43**: 69–78. Available from <https://repository.arizona.edu/handle/10150/261223> [accessed 1 April 2019].
- Horn, K.J., Thomas, R.Q., Clark, C.M., Pardo, L.H., Fenn, M.E., Lawrence, G.B., et al. 2018. Growth and survival relationships of 71 tree species with nitrogen and sulfur deposition across the conterminous U.S. *PLoS One*, **13**(10): e0205296. doi:10.1371/journal.pone.0205296. PMID:30335770.
- Janowiak, M.K., D'Amato, A.W., Swanson, C.W., Iverson, L., Thompson, F.R., Dijk, W.D., et al. 2018. New England and northern New York forest ecosystem vulnerability assessment and synthesis: a report from the New England climate change response framework project. *Gen. Tech. Rep. NRS-173*. US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA. 234 pp. doi:10.2737/nrs-gtr-173.
- Jurik, T.W., Briggs, G.M., and Gates, D.M. 1988. Springtime recovery of photosynthetic activity of white pine in Michigan. *Can. J. Bot.* **66**(1): 138–141. doi:10.1139/b88-021.
- Kipfmüller, K.F., Elliott, G.P., Larson, E.R., and Salzer, M.W. 2010. An assessment of the dendroclimatic potential of three conifer species in northern Minnesota. *Tree-ring Res.* **66**(2): 113–126. doi:10.3959/2009-12.1.
- Kosiba, A.M., Schaberg, P.G., Rayback, S.A., and Hawley, G.J. 2018. The surprising recovery of red spruce growth shows links to decreased acid deposition and elevated temperature. *Sci. Total Environ.* **637–638**: 1480–1491. doi:10.1016/j.scitotenv.2018.05.010. PMID:29801241.
- Likens, G. 2016. *Chemistry of bulk precipitation at Hubbard Brook Experimental Forest, Watershed 6, 1963–present*. Ver 9. Environmental Data Initiative. Available from <https://doi.org/10.6073/pasta/8d2d88dc718b6c5a2183cd88aae26bf1> [accessed 20 July 2020].
- Martin-Benito, D., and Pederson, N. 2015. Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. *J. Biogeogr.* **42**(5): 925–937. doi:10.1111/jbi.12462.
- Mathias, J.M., and Thomas, R.B. 2018. Disentangling the effects of acidic air pollution, atmospheric CO₂, and climate change on recent growth of red spruce trees in the Central Appalachian Mountains. *Glob. Change Biol.* **24**(9): 3938–3953. doi:10.1111/gcb.14273.
- McAvoy, T.J., Régnière, J., St-Amant, R., Schneeberger, N.F., and Salom, S.M. 2017. Mortality and recovery of hemlock woolly adelgid (*Adelges tsugae*) in response to winter temperatures and predictions for the future. *Forests*, **8**(12): 497. doi:10.3390/f8120497.
- McGregor, W.H.D., and Kramer, P.J. 1963. Seasonal trends in rates of photosynthesis and respiration of loblolly pine and white pine seedlings. *Am. J. Bot.* **50**(8): 760–765. doi:10.1002/j.1537-2197.1963.tb10643.x.
- NAPA. 2014. *Pinus strobus*. Biota of North America Program (BONAP). pp. County-level distribution map from the North American Plant Atlas (NAPA).
- National Atmospheric Deposition Program. 2017. NADP/NTN Monitoring. US Geological Survey. Available at <http://nadp.sws.uiuc.edu/data/ntn/> [accessed 11 May 2017].
- NOAA National Centers for Environmental Information. 2018. Historical Palmer drought indices. Available from <https://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers/> [accessed 21 November 2018].
- NOAA National Climatic Data Center. 2019. NOAA's gridded climate divisional dataset (CLIMDIV). Climate Divisions 1, 2 and 3. Available from <https://www7.ncdc.noaa.gov/CDODivisionalSelect.jsp> [accessed 16 May 2019].
- Nowacki, G.J., and Abrams, M.D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol. Monogr.* **67**(2): 225–249. doi:10.1890/0012-9615(1997)067[0225:RGACFR]2.0.CO;2.
- Nowosad, J. 2018. Pollen: analysis of aerobiological data. R package version 0.71.0. Available from <https://CRAN.R-project.org/package=pollen>.
- Nuckolls, A.E., Wurzbarger, N., Ford, C.R., Hendrick, R.L., Vose, J.M., and Kloeppel, B.D. 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation: impacts on the carbon cycle of southern Appalachian forests. *Ecosystems*, **12**(2): 179–190. doi:10.1007/s10021-008-9215-3.
- Ögren, E., Nilsson, T., and Sundblad, L.-G. 1997. Relationship between respiratory depletion of sugars and loss of cold hardiness in coniferous seedlings over-wintering at raised temperatures: indications of different sensitivities of spruce and pine. *Plant. Cell Environ.* **20**(2): 247–253. doi:10.1046/j.1365-3040.1997.0156.x.
- Oswald, E.M., Pontius, J., Rayback, S.A., Schaberg, P.G., Wilmot, S.H., and Dupigny-Giroux, L.-A. 2018. The complex relationship between climate and sugar maple health: Climate change implications in Vermont for a key northern hardwood species. *For. Ecol. Manage.* **422**: 303–312. doi:10.1016/j.foreco.2018.04.014.
- Paradis, A., Elkinton, J., Hayhoe, K., and Buonaccorsi, J. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitigation Adapt. Mitig. Adapt. Strateg. Glob. Change*. **13**(5–6): 541–554. doi:10.1007/s11027-007-9127-0.
- Pederson, N., Bell, A.R., Cook, E.R., Lall, U., Devineni, N., Seager, R., et al. 2013. Is an Epic pluvial masking the water insecurity of the Greater New York City Region? *J. Clim.* **26**(4): 1339–1354. doi:10.1175/JCLI-D-11-00723.1.
- Prasad, A.M., Iverson, L.R., Matthews, S., and Peters, M. 2007. Ongoing. A climate change atlas for 134 forest tree species of the eastern United States [database]. Northern Research Station, USDA Forest Service, Delaware, Ohio.
- Reinmann, A.B., Sussler, J.R., Demaria, E.M.C., and Templer, P.H. 2019. Declines in northern forest tree growth following snowpack decline and soil freezing. *Glob. Change Biol.* **25**(4): 420–430. doi:10.1111/gcb.14420.
- Rennenberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R.S., and Gessler, A. 2006. Physiological responses of forest trees to heat and drought. *Plant Biol.* **8**(5): 556–571. doi:10.1055/s-2006-924084. PMID:16773557.
- Rollinson, C.R., Alexander, M.R., Dye, A.W., Moore, D.J.P., Pederson, N., and Trouet, V. 2020. Climate sensitivity of understory trees differs from overstory trees in temperate mesic forests. *Ecology*, **102**(3): e03264. doi:10.1002/ecy.3264.
- Saladyga, T., and Maxwell, R.S. 2015. Temporal variability in climate response of eastern hemlock in the Central Appalachian Region. *Southeast. Geogr.* **55**(2): 143–163. doi:10.1353/sgo.2015.0014.
- Schaberg, P.G., Wilkinson, R.C., Shane, J.B., Donnelly, J.R., and Cali, P.F. 1995. Winter photosynthesis of red spruce from three Vermont seed sources. *Tree Physiol.* **15**(5): 345–350. doi:10.1093/treephys/15.5.345. PMID:14965959.
- Schaberg, P.G., DeHayes, D.H., and Hawley, G.J. 2001. Anthropogenic calcium depletion: a unique threat to forest ecosystem health? *Ecosyst. Health*, **7**(4): 214–228. doi:10.1046/j.1526-0992.2001.01046.x.
- Schaberg, P.G., Miller, E.K., and Eagar, C. 2010. Assessing the threat that anthropogenic calcium depletion poses to forest health and productivity. USDA Forest Service, Pacific Northwest and Southern Research Stations, Portland, Oregon, Gen. Tech. Rep. PNW-GTR-802. Available from <https://www.nrs.fs.fed.us/pubs/37004>.
- Speer, J.H. 2010. *Fundamentals of tree-ring research*. The University of Arizona Press, Tucson.

- Stern, R., Schaberg, P.G., Rayback, S.A., Murakami, P.F., Hansen, C., and Hawley, G.J. 2020. Growth of canopy red oak near its northern range limit: current trends, potential drivers, and implications for the future. *Can. J. For. Res.* **50**: 975–988. doi:10.1139/cjfr-2019-0200.
- Stokes, M., and Smiley, T. 1968. An introduction to tree-ring dating. University of Chicago Press., Chicago, IL. pp. 31–46.
- Tardif, J., Brisson, J., and Bergeron, Y. 2001. Dendroclimatic analysis of *Acer saccharum*, *Fagus grandifolia*, and *Tsuga canadensis* from an old-growth forest, southwestern Quebec. *Can. J. For. Res.* **31**(9): 1491–1501. doi:10.1139/x01-088.
- Teskey, R.O., Whitehead, D., and Linder, S. 1994. Photosynthesis and carbon gain by pines. *Ecol. Bull.* **43**: 35–49. Available from <http://www.jstor.org/stable/20113130>.
- USDA Forest Service. 2019. Northern research station and forest health protection, “alien forest pest explorer - species map.” Database last updated 24 July 2019. Available from <https://www.nrs.fs.fed.us/tools/afpe/maps/> [accessed 27 January 2021].
- USDA Natural Resources Conservation Service. 2019. Soil survey. Available from <http://nrcs.usda.gov/wps/portal/nrcs/main/soils/survey> [accessed 16 May 2019].
- US Global Change Research Program, 2018. Impacts, risks, and adaptation in the united states: fourth national climate assessment, Volume II. Edited by D.R. Reidmiller, C.W. Avery, D.R. Easterling, K.E. Kunkel, K.L.M. Lewis, T.K. Maycock, and B.C. Stewart. U.S. Global Change Research Program. Available from https://nca2018.globalchange.gov/downloads/NCA4_Report-in-Brief.pdf [accessed 10 August 2019].
- Vermont Department of Forests Parks and Recreation, 2020. Vermont forest health highlights. Available from https://fpr.vermont.gov/sites/fpr/files/doc_library/2020%20VT%20Forest%20Health%20Highlights_PDF%20compact%20version.pdf [accessed 25 January 2021].
- Vicente-Serrano, S.M., Beguería, S., and López-Moreno, J.I., 2017. Global SPEI database. Available from <http://spei.csic.es/database.html> [accessed 10 July 2017].
- West, P.W. 1980. Use of diameter increment and basal area increment in tree growth studies. *Can. J. For. Res.* **10**(1): 71–77. doi:10.1139/x80-012.
- Wigley, T.M., Briffa, K.R., and Jones, P.D. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydro-meteorology. *J. Climate Appl. Meteor.* **23**(2): 201–213. doi:10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2.
- Wyka, S.A., Smith, C., Munck, I.A., Rock, B.N., Ziniti, B.L., and Broders, K. 2017. Emergence of white pine needle damage in the northeastern United States is associated with changes in pathogen pressure in response to climate change. *Glob. Change Biol.* **23**(1): 394–405. doi:10.1111/gcb.13359.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* **21**(3): 414–416. doi:10.1139/x91-053.
- Zang, C., and Biondi, F. 2015. Treeclim: an R package for the numerical calibration of proxy-climate relationships. *Ecography*, **38**(4): 431–436. doi:10.1111/ecog.01335.