Exploring Environmental Drivers of Growth for Tree Species Associated with a Rare Limestone Bluff Cedar–Pine Forest in Vermont

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Abstract - The limestone bluff cedar–pine forest is a rare upland natural community that is threatened by development and invasion by exotic species. Furthermore, the sensitivity of this forest-type to changes in climate and pollution exposure is unknown. We collected xylem increment cores from 4 conifer species (*Thuja occidentalis* [Northern White Cedar], *Juniperus virginiana* [Eastern Red Cedar], *Pinus strobus* [Eastern White Pine], and *Tsuga canadensis* [Eastern Hemlock]) and 4 hardwood species (*Quercus rubrum* [Northern Red Oak], *Quercus alba* [White Oak], *Fagus grandifolia* [American Beech], and *Fraxinus americana* [White Ash]) within and close to a cedar–pine forest along the eastern shore of Lake Champlain in Vermont and correlated radial tree growth to precipitation, snow, temperature, and pollution data to assess which factors influenced growth during the time period 1937–2016. We examined growth and possible environmental drivers of it for a variety of species to evaluate how unique these may be for the cedar and pine trees emblematic of the limestone-bluff community. For both conifers and hardwoods, precipitation exhibited the strongest positive correlations with growth and occurred with greater frequency compared to other climate and pollution parameters. Snow was positively associated and temperature was negatively associated with growth for all species. Despite growing over calcium-rich bedrock, and especially for the conifers, pollution seemed to limit growth in years prior to pollution reductions enacted following the 1990 Amendments to the Clean Air Act.

Introduction

The limestone bluff cedar–pine forest is a rare upland natural community type in Vermont that is characterized by an overstory of cedars (*Thuja occidentalis* L. [Northern White Cedar] and *Juniperus virginiana* L. [Eastern Red Cedar]), pines (primarily *Pinus strobus* L. [Eastern White Pine]) and a variety of other conifer and hardwood species occurring in lesser numbers or in immediately adjacent transition hardwood limestone bluff forests (Mazowita 2013, Sorenson and Popp 2007). Although they include various species, these forests are characterized by dark bands of conifers highly exposed to winds that can result in stunted, twisted stems. Limestone bluff cedar–pine forests occur on thin soils overlaying calcareous bedrock, and in Vermont they exist primarily along the shores of Lake Champlain

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(Sorenson and Popp 2007). These forests contain an unusually high concentration of rare, threatened, and endangered plant species, including the state-threatened *Cypripedium arietinum* R. Br. (Ram's Head Lady-slipper) (Sorenson and Popp 2007). These woodlands also provide important wildlife habitat in the highly developed and agricultural Champlain Valley (Sorenson and Popp 2007), including many species of birds that have been identified by Audubon Vermont as being a high priority for protection in northeastern forests (Mazowita 2013).

Vermont limestone bluff cedar–pine forests are few in number and size, with a total of 97 patches identified throughout Vermont in a broad landscape analysis, of which 72% were under 4 ha (10 ac) (Sorenson and Popp 2007). Indeed, there are only 21 limestone bluff cedar–pine forests in Vermont that are considered state-significant based on evaluations of the size and current condition of forests and the quality of surrounding landscapes (Sorenson and Popp 2007). Furthermore, due to their picturesque lakeside settings, these forests are highly threatened by development (Sorenson and Popp 2007). Because they occur on calcium-rich limestone and dolomite bluffs, these forests are also especially sensitive to invasion by exotic plant species (e.g., *Rhamnus cathartica* L. [Common Buckthorn], *Lonicera morrowii* Gray [European Bush Honeysuckle], and *Berberis vulgaris* L. [Common Barberry]) following disturbance (Sorenson and Popp 2007). Considering their scarcity, propensity to harbor rare species, and the persistent threat from development and exotic species encroachment, limestone bluff cedar–pine forests are a conservation priority within Vermont (Sorenson and Popp 2007).

Although there are multiple known threats to limestone bluff cedar–pine forests, it is less clear how changes in temperature and precipitation associated with climate change might alter the health and productivity of tree species within these forests. Over the past century, both temperature and total annual precipitation levels have increased in the Northeast—a process that is projected to continue through the 21st century (Janowiak et al. 2018). Since 1900, Vermont has experienced an increase in annual average temperature of 1.1 °C and in average annual precipitation of 21% (Clark and Crossett 2021). The most dramatic change in Vermont's climate has occurred during the winter months. Since 1960, winter temperatures have warmed 2.5 times faster than annual temperatures, and winter precipitation has increased overall, though less falls as snow (Clark and Crossett 2021).

Projections of how climate change may alter the suitable habitat of tree species common to limestone bluff cedar–pine forests of the Champlain Valley are mixed, with some projected to experience increases (e.g., Eastern Red Cedar, *Quercus rubra* L. [Northern Red Oak] and *Quercus alba* L. [White Oak]) whereas others (e.g., Northern White Cedar, Eastern White Pine, and *Tsuga canadensis* (L.) Carr. [Eastern Hemlock]) may face challenges in Vermont as the climate continues to change (Prasad et al. 2007–ongoing, Wikle et al. 2021). However, direct evidence of the climate sensitivity of trees within limestone bluff cedar–pine forests is lacking.

Another changing environmental parameter that could influence the health and productivity of these forests is pollution loading of sulfate, nitrate, and hydrogen ions associated with acid deposition. While pollution inputs have declined since the

1990 amendments to the Clean Air Act, acid deposition has been shown to negatively impact the long-term health and growth of multiple conifer and hardwood species (e.g., Halman et al. 2011, 2015; Schaberg et al. 2001). The tree-species mix, elevation, and base-rich substrate underlying limestone bluff cedar–pine forests are not consistent with conditions commonly associated with acid-deposition impacts (e.g., Schaberg et al. 2010). However, recent research has shown that some forests in the Champlain Valley show a greater sensitivity to historic pollution loading than once realized (Stern et al. 2020).

Understanding how changes in environmental conditions are affecting tree communities is crucial to managing iconic northeastern forests (Swanston et al. 2018), particularly for preserving unique threatened woodlands like limestone bluff cedar–pine forests. To add to that understanding, we assessed the relative moisture (precipitation and snow), temperature, and pollution sensitivity of a limestone bluff cedar–pine forest and its adjacent forest communities by measuring tree radial growth via tree-ring analysis of 4 conifer species (Northern White Cedar, Eastern Red Cedar, Eastern White Pine, and Eastern Hemlock) and 4 hardwood species (Northern Red Oak, White Oak, *Fagus grandifolia* Ehrh. [American Beech], and *Fraxinus americana* L. [White Ash]) at a Vermont state-significant limestone bluff cedar–pine forest in Red Rocks Park in South Burlington, VT. We used xylem growth to compare the age and productivity of each species and identify moisture and temperature conditions and pollution inputs best associated with species-specific variations in growth. We examined a broad spectrum of tree species to evaluate if patterns noted for the cedars and pines that dominate limestone-bluff forests were distinct to these or are similar to those detected for nearby conifer and hardwood species.

Overall, we hypothesized that:

(H_1) thin soils with limited moisture-holding capacity within limestone bluff cedar–pine forests would cause resident trees to be particularly susceptible to growth reductions associated with drought/low precipitation;

(H_2) thin soils that result in shallow roots would make trees more vulnerable to root freezing injury that reduces aboveground growth when insulative/protective snow is limited;

(H_3) trees within the limestone bluff cedar–pine forest at Red Rocks Park would generally show few constraints in growth associated with heat exposure because they reside next to Lake Champlain, a large body of water that moderates temperature levels;

(H_4) conifers within limestone bluff cedar–pine forests would benefit from extended carbon capture during warm spring and autumn seasons, which would result in increased radial growth; and

(H_5) because the limestone bluff cedar–pine forest of Red Rocks Park overlies calcium-rich bedrock at a low elevation that historically received low inputs of pollution deposition, and because it is comprised of species with little recorded sensitivity to acid deposition, its trees would show little sensitivity to pollution loading.

Field-site Description

Red Rocks Park is located in South Burlington, VT, along the eastern shore of Lake Champlain (44°26'42"N, 73°13'38"W; Fig. 1). It is a 40.5-ha (100-ac) forested natural area managed by the South Burlington Recreation and Parks Department and aptly named for its reddish, iron-rich rock, Monkton Quartzite. The forest is comprised of several natural communities, the most prevalent being the mesic maple–ash–hickory–oak forest (Mazowita 2013, Thompson et al. 2019). The state-significant limestone bluff cedar–pine forest is located along the southern and western edges of the park. Soils of Red Rocks Park are mostly loams that are rich in nutrients, particularly calcium, due to underlying limestone bedrock (Mazowita 2013). However, soils here also tend to be quite shallow (typically <0.61 m (<2 ft) deep), with many rock exposures (Mazowita 2013). During the timeframe of our study (1937–2016), average monthly temperatures in the park varied from a maximum of 27.2 °C (Tmax, July) to a minimum of -12.5 °C (Tmin, January), while average monthly precipitation varied from a maximum of 9.53 cm (July) to a minimum of 4.56 cm (February) (Fig. 2; PRISM Climate Group 2020). In addition, average monthly snowfall varied from a maximum of 47.8 cm (January) to a minimum of 0.003 cm (September), and average monthly snow duration (# of days when snow was >2.54 cm) varied from 21.6 days (January) to 0.05 days

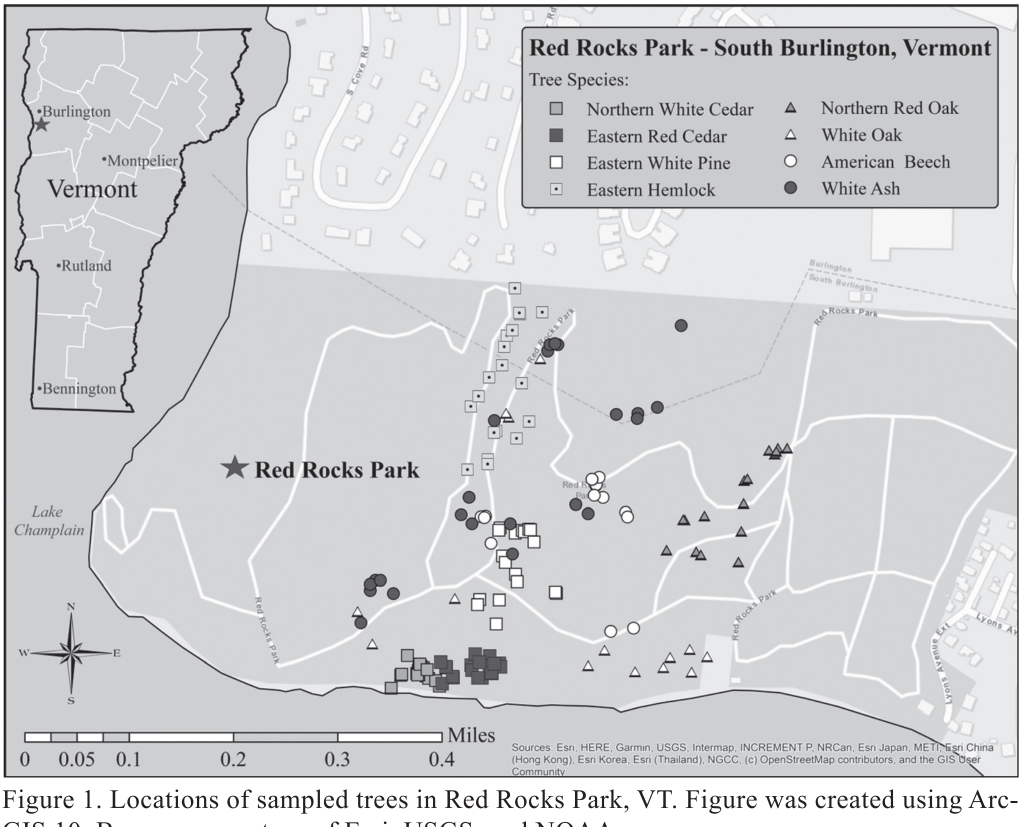

Figure 1. Locations of sampled trees in Red Rocks Park, VT. Figure was created using ArcGIS 10. Base map courtesy of Esri, USGS, and NOAA.

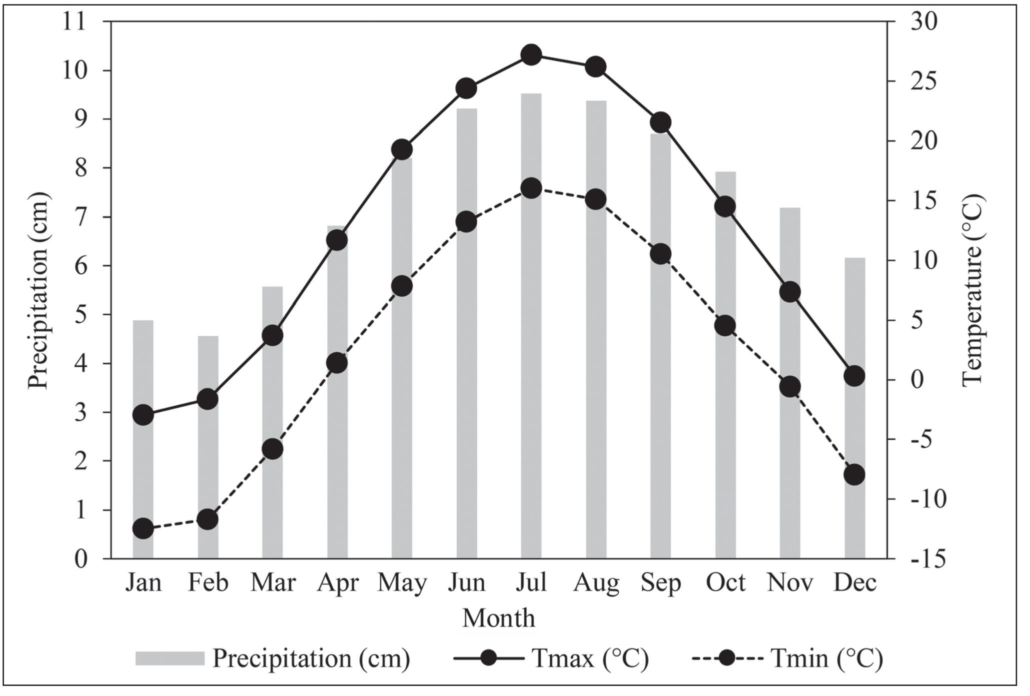

Figure 2. Average monthly precipitation (cm) and mean maximum temperature (Tmax; °C) and minimum temperature (Tmin; °C) for Burlington, VT, from 1937 to 2016 (NOAA National Climatic Data Center 2018).

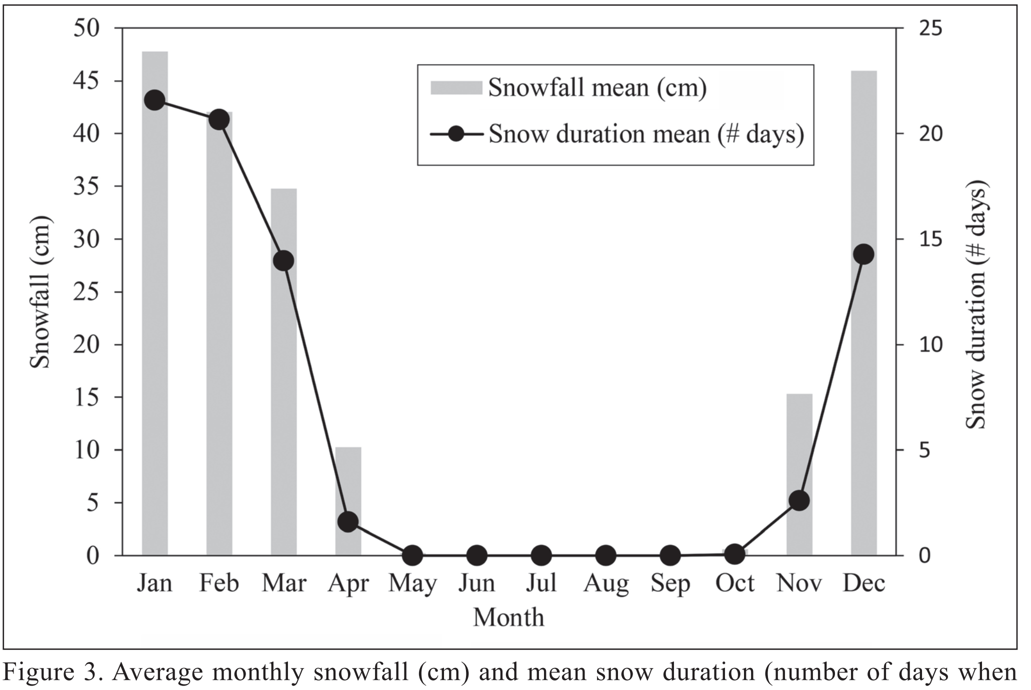

Figure 3. Average monthly snowfall (cm) and mean snow duration (number of days when snow depth was greater than 2.54 cm) for Burlington, VT, from 1937 to 2016 (Applied Climate Information System 2021).

(October) (Fig. 3; Applied Climate Information System 2021). Historical land-use records indicate that Red Rocks Park retained several owners from 1798 through 1971 when it became a public park (Mazowita 2013). One such landowner, Edward Hatch (proprietor of New York City's department store Lord & Taylor), established 4.0 km (2.5 mi) of carriage roads in the early 1890s that currently exist as a popular and widely used trail system. Today, the park is used by the local community for several types of outdoor activities including hiking, birding, swimming, snowshoeing, and enjoying the expansive views of Lake Champlain and the Adirondack Mountains of New York. Our study was limited to the central portion of the park, which, except for the trail system, appeared least impacted by human disturbance, including no known tree harvests post trail development. Restricting increment-core sampling to this intact, forested area provided us the best opportunity to capture changes in tree growth associated with climate and pollution inputs rather than direct human disturbance.

Methods

Dendrochronology

We collected increment cores in 2016, 2017, and 2019 from 142 dominant and codominant Northern White Cedar (19 trees), Eastern Red Cedar (19), Eastern White Pine (18), Eastern Hemlock (19), Northern Red Oak (16), White Oak (15), American Beech (15), and White Ash (24) trees (Fig. 1). We opportunistically located trees and avoided individuals with observable bole or crown damage to better characterize average growth and minimize the influence of non-climatic factors on growth. We extracted 2 xylem increment cores (diameter of 5 mm) at breast height (1.3 m above the soil surface) from opposite sides of each tree and perpendicular to the slope. We carefully placed cores in labeled drinking straws for safe transport to the laboratory. We also measured diameter at breast height (DBH; cm) of each tree and recorded this value for subsequent determination of annual basal area increment (BAI; cm^2).

We processed increment cores by oven-drying, mounting on grooved wooden blocks, and sanding them with progressively finer sandpaper (200 to 800 grit). We visually crossdated annual rings under a stereoscope by noting years of narrow ring growth and using this information to account for missing and/or locally absent rings among all cores (known as the list method; Yamaguchi 1991). We meassured individual ring widths (to a precision of 0.001 mm) using a Velmex sliding stage unit (Velmex Inc., Bloomfield, NY) and MeasureJ2X software (VoorTech Consulting, Holderness, NH). We employed the computer program COFECHA to confirm the accuracy of visual crossdating and detect errors in ring-width measurements using segmented time-series correlation analyses (Grissino-Mayer 2001, Holmes 1983). Individual ring widths were averaged per tree and used to calculate annual radial growth, expressed as BAI, using function 'bai.out' in R package 'dplR' (Bunn et al. 2016).

In preparation for analyses of growth with climate (moisture and temperature) and pollution deposition, we used ring-width measurements to evaluate for possible disturbance events using the function ‘growthAveragingALL’ in R package ‘TRADER’ (Altman et al. 2014, Fibich et al. 2017). We then detrended individual species’ chronologies using either Friedman’s Super Smoother (Friedman 1984, Pederson et al. 2013) if at least 25% of trees exhibited a major release event (Eastern Red Cedar, White Ash) or a 67%*n* cubic smoothing spline (Cook and Peters 1981) if less than 25% of trees exhibited a major release event (Northern White Cedar, Eastern White Pine, Eastern Hemlock, Northern Red Oak, White Oak, American Beech) within a 10-year timeframe using the function ‘detrend’ in R package ‘dplR’ (Bunn et al. 2016). Detrending minimizes the local effects of site differences, competition, and tree age on growth, thereby preserving climate signals within a tree’s chronology. We standardized the detrended chronologies to create a stand-wide residual chronology with a Tukey’s biweight robust mean resulting in a ring-width index (RWI) chronology for each species using the function ‘chron’ in R package ‘dplR’ (Bunn et al. 2016). We truncated all RWI chronologies to 1937 based on the calculated expressed population signal of the shortest chronology (Northern Red Oak) and using a cutoff of 0.80 with the function ‘rwi.stats.running’ in R package ‘dplR’ (Bunn et al. 2016) in order to establish a common time period for subsequent analyses of growth with climate and deposition parameters.

Statistical analyses

We associated stand-wide growth for each species with seasonal precipitation, snow, and temperature metrics beginning the spring prior to ring formation (since climate conditions in one year can affect tree growth in the subsequent year) through autumn of the year of ring formation (pSpring = March, April, May of prior year; pSummer = June, July, August of prior year; pAutumn = September, October, November of prior year; Winter = December, January, February; Spring = March, April, May; Summer = June, July, August; Autumn = September, October, November) using RWIs and 25-year moving Pearson’s correlations with the function ‘dcc’ in R package ‘treeclim’ (Zhang and Bondi 2015). We obtained monthly precipitation (Precip; cm), maximum temperature (Tmax; °C), and minimum temperature (Tmin; °C) data from 1937 to 2016 from PRISM Climate Group (2020). We obtained monthly total snowfall (cm) and snow duration (number of days when snow depth was >2.54 cm) data from NOAA Online Weather Data (Applied Climate Information System 2021). For comparisons of growth with pollution-deposition data (SO_4^{2-}, NO_3^-, and rainfall pH), we used a 10-year moving-correlation window using data obtained from the National Atmospheric Deposition Program (2021). The use of a shorter moving window was necessary due to the limited availability of pollution-deposition data (1965–2016). In reporting the results of moving correlations, the date listed is the last year of the 25-year (or in the case of pollution data, 10-year) period for which correlations were significantly associated with growth.

Results

Age, size, and growth comparisons

The trees in and around the Red Rocks Park limestone bluff cedar–pine forest exhibited a variety of sizes; the largest diameters being 50+ cm DBH (Eastern

White Pine, Northern Red Oak, White Oak and Eastern Hemlock) and the smallest <30 cm DBH (Northern White Cedar and Eastern Red Cedar) (Table 1). White Ash and American Beech were intermediate in size (both ~37 cm DBH). Average tree age also varied widely, with the youngest estimated average age <100 years (Northern Red Oak and White Ash) and the oldest >200 years (White Oak). As a group, conifers had a higher average age (156.4 years) than hardwoods (136.4 years) even though hardwoods included White Oak, with the highest species mean (213.5 years) and oldest individual tree (~386 years). Patterns of growth also differed greatly among the species, from low growth and limited yearly variation in annual BAI for the cedars to high growth and greater year-to-year variation for Eastern White Pine, Eastern Hemlock, and Northern Red Oak (Fig. 4). In recent years, Red Oak growth has been particularly robust. In contrast, White Oak and White Ash have exhibited intermediate levels of growth and growth variation, whereas American Beech exhibited constrained growth for the entire chronology.

Correlations of growth with environmental data

Precipitation. Precipitation the autumn before and the winter, spring, and summer of ring formation was broadly and positively associated with growth (Table 2). This result was evident for both conifers and hardwoods. Positive correlations between growth and winter, spring, and summer precipitation were particularly evident for coniferous species. Notably, Eastern Hemlock growth responded favorably to precipitation inputs for a cumulative total of 19 years in winter (from 1995 to 2015), 16 years in spring (from 1973 to 2004), and 45 years in summer (from 1964 to 2016). Likewise, Eastern White Pine growth exhibited positive associations with spring precipitation for a total of 48 years (from 1961 to 2016) and with summer precipitation for 43 years (from 1974 to 2016). Among the hardwood species, summer precipitation influenced the longest periods of positive growth for all 4 species during the time period 1961–2016 (Northern Red Oak: 15 years; White Oak: 27 years; American Beech: 41 years; White Ash: 36 years). In contrast, precipitation the spring and summer before and the autumn of ring formation were often negatively associated with growth for both conifers and hardwoods.

Table 1. Summary of chronology statistics obtained from increment cores of 8 tree species growing in Red Rocks Park, South Burlington, VT.

Species	Trees (*n*)	Cores (*n*)	Average DBH (cm)	Average minimum age (yrs)	Year of oldest measured tree ring	EPS > 0.80
Northern White Cedar	19	37	29.4	157.3	1836	1883
Eastern Red Cedar	19	39	26.9	163.6	1763	1838
Eastern White Pine	18	38	56.6	130.3	1872	1882
Eastern Hemlock	19	39	50.1	174.3	1803	1807
Northern Red Oak	16	31	54.1	98.6	1897	1912
White Oak	15	29	51.6	213.5	1630	1792
American Beech	15	31	36.5	133.9	1826	1897
White Ash	24	48	36.8	99.9	1885	1930

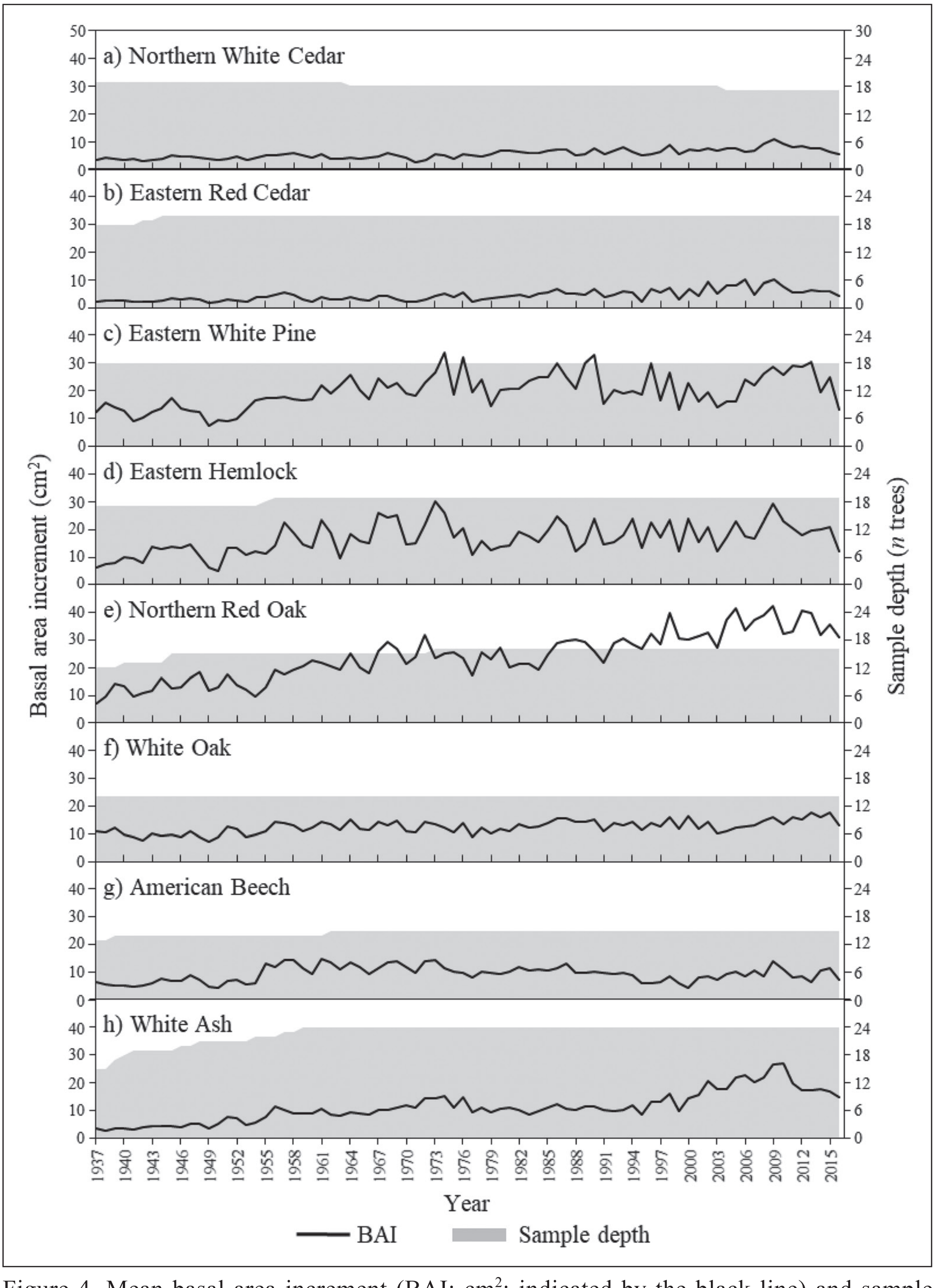

Figure 4. Mean basal area increment (BAI; cm^2; indicated by the black line) and sample depth (*n* trees; indicated by grey shaded area) of (a) Northern White Cedar, (b) Eastern Red Cedar, (c) Eastern White Pine, (d) Eastern Hemlock, (e) Northern Red Oak, (f) White Oak, (g) American Beech, and (h) White Ash from 1937 to 2016. Dates indicate the last year of a 25-year moving window.

Table 2. Significant seasonal correlations of radial growth with precipitation for (A) 4 conifer and (B) 4 hardwood species ($P \leq 0.05$) from 1937 to 2016. Years listed indicate the last year of a 25-year moving window for which correlations were conducted. Correlation coefficients (*r*) represent the highest or lowest *r* for a single year or span of years. ns indicates season with no significant correlations. [Table continued on next page.]

A.	Northern White Cedar		Eastern Red Cedar		Eastern White Pine		Eastern Hemlock	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
pSpring	ns		2008–2016	–0.444	2009–2011	-0.383	2013–2015	–0.350
pSummer					1967–1971	-0.363		
					1999–2001	-0.502		
					2003	-0.448		
					2005	-0.398	1964–1972	-0.469
	1998–2008	-0.514	1999–2004	–0.558	2007	-0.352	1999–2004	-0.531
pAutumn	1964	0.350					1978	-0.294
	1966	0.356	ns		2016	0.338	1999–2001	0.399
Winter							1995–2001	0.404
	2004–2010	0.564	1996–2006	0.459			2003–2013	0.442
	2012	0.394	2012	0.306	2014–2015	0.321	2015	0.373
Spring							1973	0.381
					1961–1990	0.702	1976–1983	0.466
					1992–1998	0.408	1988	0.297
			1965–1969	0.452	2000	0.341	1995–1997	0.404
	1978–1980	0.462	1976–1984	0.481	2006–2008	0.384	2000–2001	0.389
	1982–1986	0.395	2008–2010	0.439	2010–2016	0.472	2003–2004	0.378
Summer	1961	0.330						
	1999–2000	0.562					1964	0.318
	2004–2005	0.503	1993–1994	0.409			1972–1977	0.437
	2008–2011	0.499	1996–2016	0.643	1974–2016	0.703	1979–2016	0.732
Autumn							1983	-0.398
	2013–2015	-0.385	1999–2000	-0.491	1979–1983	-0.427	1999–2000	0.448

B.	Northern Red Oak		White Oak		American Beech		White Ash	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
pSpring			1997–1998	-0.348				
			2001	-0.356			1961–1965	-0.355
			2004	-0.316			2000	-0.298
	1961–1963	-0.336	2006	-0.354	1974	0.365	2013	-0.270
	1965	-0.315	2009–2011	-0.399	2007–2008	0.449	2015	-0.271
pSummer			1981–1987	-0.427				
			1991–2008	-0.707				
	1999	-0.451	2016	-0.399	ns		1999–2003	-0.545
pAutumn	1961–1962	0.277	1997–2002	0.453	1999	0.383	1999–2000	0.402
Winter							1986–1988	0.452
					2012	0.275	2010	0.369
	2008–2016	0.500	2014	0.396	2014–2015	0.326	2013–2016	0.482
Spring			1978–1982	0.403			1987–1982	0.540
	1994	-0.303	2016	0.399	1978–1982	0.426	2010	0.418

Snow. Winter snowfall (Table 3) was positively associated with growth for all 8 species. Eastern Red Cedar (15 years), Eastern Hemlock (22 years), and American Beech (20 years) exhibited the longest cumulative period of significant

Table 2, continued.

	Northern Red Oak		White Oak		American Beech		White Ash	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
Summer					1961–1970	0.472		
					1972–1977	0.463		
					1981–1984	0.423		
			1981–2003	0.594	1987–2006	0.453		
	2002–2016	0.700	2013–2016	0.485	2010	0.265	1981–2016	0.658
Autumn	1978	-0.510						
	1983	-0.481						
	1991–1996	-0.511	1978–1982	-0.546				
	1998–2000	-0.473	1995–2000	-0.604	1996–1999	-0.607	ns	

Table 3. Significant seasonal correlations of radial growth with snowfall for (A) 4 conifer and (B) 4 hardwood species ($P \leq 0.05$) from 1937 to 2016. Years listed indicate the last year of a 25-year moving window for which correlations were conducted. Correlation coefficients (*r*) represent the highest or lowest *r* for a single year or span of years. ns indicates season with no significant correlations.

A.	Northern White Cedar		Eastern Red Cedar		Eastern White Pine		Eastern Hemlock	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
pAutumn			1975	-0.333				
			1978–1980	-0.422				
			1982	-0.397				
			1985	-0.352	1976–1978	-0.377		
			1988	-0.352	1990	-0.312		
	ns		1990	-0.403	1997–1998	-0.340	ns	
Winter			1996–2001	0.497				
			2003–2006	0.439				
			2008–2010	0.432				
			2013	0.324				
	2005–2013	0.560	2015	0.342	2014–2016	0.391	1995–2016	0.582
Spring	1987	-0.484	ns		1970	0.546	ns	

B.	Northern Red Oak		White Oak		American Beech		White Ash	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
pAutumn	ns		ns		2002	0.385	ns	
Winter	2005–2011	0.604					2010	0.403
	2013	0.420			1996–1997	0.303	2012	0.360
	2015–2016	0.446	1974–1975	-0.445	1999–2016	0.420	2014–2016	0.457
Spring	1969–1970	0.412						
	1972–1974	0.355						
	1976–1977	0.338			1961–1963	0.421		
	1979	0.323	1966–1970	0.457	1967–1970	0.558	ns	

relationships with snowfall occurring from 1995 to 2016. Spring snowfall resulted in positive growth in 3 of the hardwood species: Northern Red Oak, White Oak, and American Beech. Among the conifers, only Eastern White Pine growth had a positive relationship with spring snowfall, and this correlation was of limited duration (just 1 year). Winter snow duration (Table 4) was also broadly and positively associated with growth for both conifer and hardwood species, with American Beech having the largest cumulative period of significant associations (16 years from 1979 to 2016). Negative associations between snow duration and growth were mostly noted for conifers during the fall and spring shoulder seasons.

Temperature. For most species and seasons, Tmax was negatively correlated with growth (Table 5). This negative association was particularly evident for summer and autumn Tmax during the year of ring formation, with all 4 conifer species exhibiting the longest cumulative period of negative associations during the summer season (20–31 years from 1961 to 2016). Additionally, Northern White Cedar had an extended period of negative growth associated with autumn Tmax (17 years from 1987 to 2016). Among the hardwood species, White Oak experienced

Table 4. Significant seasonal correlations of radial growth with snow duration for (A) 4 conifer and (B) 4 hardwood species ($P \leq 0.05$) from 1937 to 2016. Years listed indicate the last year of a 25-year moving window for which correlations were conducted. Correlation coefficients (*r*) represent the highest or lowest *r* for a single year or span of years. ns indicates season with no significant correlations.

A.	Northern White Cedar		Eastern Red Cedar		Eastern White Pine		Eastern Hemlock	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
pAutumn					1976–2000	-0.548		
			1990–1991	-0.402	2003	-0.416		
			1993	-0.374	2010	-0.396	2005–2011	-0.425
	ns		1996–1997	-0.316	2013	-0.393	2014	-0.399
Winter			1978–1979	-0.397				
			2004–2005	0.426				
	2007–2010	0.417	2007–2010	0.418	1965	0.379	ns	
Spring			1981	-0.427				
	1981–1988	-0.640	1983–1992	-0.573				
	1990	-0.545	2009–2010	-0.383	1978	-0.318	1974	-0.333

B.	Northern Red Oak		White Oak		American Beech		White Ash	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
pAutumn			1994	-0.390				
			1996–1997	-0.436				
	ns		2003	-0.481	ns		ns	
Winter					1979	-0.376		
	1965–1970	0.425			2001–2011	0.515		
	2005–2011	0.479	ns		2013–2016	0.430	2013–2016	0.377
Spring							2000	-0.301
							2003–2007	-0.339
	1961–1963	0.471	ns		2001–2002	0.358	2009–2013	-0.353

a prolonged period of negative associations of growth with summer Tmax (mostly from 1992 to 2016). However, noted exceptions to this pattern were limited time periods during the spring when Tmax was positively associated with growth for

Table 5. Significant seasonal correlations of radial growth with Tmax for (A) 4 conifer and (B) 4 hardwood species ($P \leq 0.05$) from 1937 to 2016. Years listed indicate the last year of a 25-year moving window for which correlations were conducted. Correlation coefficients (*r*) represent the highest or lowest *r* for a single year or span of years. ns indicates season with no significant correlations. [Table continued on next page.]

A.	Northern White Cedar		Eastern Red Cedar		Eastern White Pine		Eastern Hemlock	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
pSpring	2001	-0.426	1999–2001	-0.350				
	2005	-0.447	2007–2008	-0.370			1968	-0.321
	2012	-0.445	2011	-0.345	ns		1973–1974	-0.442
pSummer					2008–2009	0.377		
	ns		1985	0.540	2011–2016	0.520	ns	
pAutumn					1979	0.385		
					1982–1990	0.457		
					1998	0.318		
	1962	-0.264	ns		2014	0.257	ns	
Winter			1961	-0.429				
	ns		1968	-0.435	1966–1967	-0.456	ns	
Spring	1981–1983	0.371						
	1985–1994	0.518	ns		ns		ns	
Summer			1961–1964	-0.469	1965	-0.430		
			1972	-0.369	1971	-0.452	1961–1972	-0.533
	1997–2016	-0.650	1999–2016	-0.690	1999–2016	-0.531	1998–2016	-0.710
Autumn	1987	-0.412						
	1991–1997	-0.419						
	1999	-0.421						
	2001–2004	-0.439	2007	-0.394			1986–1987	-0.355
	2013–2016	-0.480	2016	-0.376	1986–1996	-0.497	2016	-0.363

B.	Northern Red Oak		White Oak		American Beech		White Ash	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
pSpring	1997	0.409	ns		1973	-0.339	ns	
pSummer			1980	0.386				
	ns		2011–2016	0.483	2002–2016	-0.473	1985	0.458
pAutumn					1978–1982	0.509		
	1979–1988	0.616	1975–1992	0.656	2002–2016	-0.548	ns	
Winter					1962	-0.534		
					1964–1965	-0.523		
					1967–1970	-0.541		
					2002	-0.407		
	1961–1962	-0.510			2004–2011	-0.396		
	1964–1973	-0.524	ns		2015–2016	-0.364	ns	

Northern White Cedar. Significant correlations of growth and Tmax for seasons the year prior to ring formation were fewer in number and showed more mixed associations with growth. For the conifers, there were slightly more negative correlations with growth, and these were mostly for Tmax in the previous spring, except that Eastern White Pine exhibited positive trends with Tmax in both the previous summer and previous autumn. Hardwoods showed more positive associations between Tmax the year before ring formation and growth, and these correlations were scattered across the seasons. A prolonged period of positive growth associated with previous autumn Tmax occurred in White Oak (18 years from 1975 to 1992).

For most species and seasons, Tmin was also negatively associated with growth (Table 6), especially during the year of ring formation. Eastern White Pine (20 years from 1975 to 1994) and both oak species (26 years from 1972 to 1997) experienced the longest period of negative growth associated with autumn Tmin. The noted exception to this pattern was Northern White Cedar, for which growth was positively associated with spring Tmin. Negative associations of growth and Tmin the year prior to ring formation were more common for conifers; however, there were limited time periods when Eastern Red Cedar (pSummer) and Eastern White Pine (pSummer and pAutumn) growth showed a positive association with Tmin. A prolonged period of positive growth with previous autumn Tmin also occurred in White Oak (16 years from 1978 to 1993).

Pollutant deposition. In general, pollution deposition showed more correlations with growth for conifer species than with hardwoods (Table 7). Nitrate deposition was negatively correlated with growth during 1 or more time periods for all species. However, there was 1 year (1987) when it was also positively associated with growth in both Northern White Cedar and White Ash. Sulfate deposition was negatively correlated with growth for all 4 conifer species during a period of known high pollutant loading in the Northeast, but it was not correlated with growth for hardwoods during the same timeframe. Precipitation pH was positively correlated with growth for all 4 conifer species as well as White Oak and American Beech during the peak of acid deposition inputs (~1980s: Driscoll et al 2001, Kosiba et

Table 5, continued.

	Northern Red Oak		White Oak		American Beech		White Ash	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
Spring							1961–1965	-0.503
	1961–1963	-0.441	1961–1969	-0.605	ns		1967	-0.323
Summer	1973	-0.432					1999–2005	-0.634
	1992	-0.356			1972–1973	-0.531	2007	-0.514
	2002–2004	-0.497			1982	-0.363	2009	-0.545
	2006	-0.393	1972–1973	-0.422	1988	-0.350	2012	-0.481
	2008–2011	-0.465	1992–2016	-0.799	1999	-0.458	2016	-0.471
Autumn	1986–1987	-0.322						
	1989–1997	-0.472	1986–1987	-0.405				
	2000	-0.320	2003–2004	-0.441				
	2002–2003	-0.432	2006–2010	-0.505	ns		1986–1999	-0.592

Table 6. Significant seasonal correlations of radial growth with Tmin for (A) 4 conifer and (B) 4 hardwood species ($P \leq 0.05$) from 1937-2016. Years listed indicate the last year of a 25-year moving window for which correlations were conducted. Correlation coefficients (*r*) represent the highest or lowest *r* for a single year or range of years. ns indicates season with no significant correlations.

A.	Northern White Cedar		Eastern Red Cedar		Eastern White Pine		Eastern Hemlock	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
pSpring							1988	-0.367
							1996	-0.366
							1999	-0.311
							2002–2004	-0.388
	2005	-0.424	1999–2004	-0.417			2008	-0.333
	2009–2014	-0.462	2006–2015	-0.513	ns		2011	-0.302
pSummer	1999	-0.359						
	2003	-0.317						
	2006–2008	-0.420						
	2010	-0.384	1986 –1990	0.463	2012–2013	0.341		
	2013–2016	-0.505	1992	0.384	2015	0.342	ns	
pAutumn	2014–2016	-0.482	ns		1987–1989	0.416	ns	
Winter							1996–1997	-0.317
			1961–1962	-0.443			1999	-0.333
	ns		1966–1969	-0.464	1999	-0.359	2006–2007	-0.340
Spring	1979–1983	0.417						
	1985–1990	0.496	ns		ns		ns	
Summer							1961–1962	-0.393
							1999	-0.346
	2006–2016	-0.475	ns		ns		2003–2004	-0.428
Autumn	2016	-0.388	ns		1975–1994	-0.583	1986–1988	-0.376

B.	Northern Red Oak		White Oak		American Beech		White Ash	
Season	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*	Year(s)	*r*
pSpring	ns		ns		ns		ns	
pSummer					2001	-0.429		
					2003–2008	-0.500		
	ns		ns		2013	-0.331	1986–1990	0.526
pAutumn					2004–2008	-0.584		
					2011	-0.369		
	1979–1989	0.531			2013–2014	-0.362		
	2005–2008	-0.442	1978–1993	0.530	2016	-0.310	1980	0.400
Winter	1961–1962	-0.448			1967–1968	-0.488		
	1965–1970	-0.449			2002–2011	-0.431		
	1972–1973	-0.377	ns		2013–2016	-0.363	ns	
Spring	1961–1962	-0.365						
	1977	-0.449						
	1979	-0.432			1996	-0.401		
	1990–1996	-0.608	1996	-0.493	2000–2002	-0.409	ns	
Summer	1992	-0.280	1992–2010	-0.528	1998–1999	-0.453	ns	
Autumn	1972–1997	-0.639	1972–1997	-0.641	1986–1995	-0.479	1986–1997	-0.599

al. 2018). However, in more recent times, significant negative associations between precipitation pH and growth occurred with Northern White Cedar (2016) and Northern Red Oak (2013–2016).

Discussion

Tree age and growth

The trees in and around the Red Rocks Park limestone bluff cedar–pine forest showed a wide variation in age, size, and growth that reflect both the historical land use of the site and the diversity of silvics of component tree species. For example, the oldest and largest trees were White Oak (intermediate in shade tolerance) and Eastern Hemlock (highly shade tolerant) that were clustered in a portion of the park that is thought to have had limited harvesting or management (Mazowita 2013). Indeed, the oldest tree assessed was a White Oak that had visible rings dated to the year 1630. Because our increment core samples of this ancient tree did not reach pith, we estimated (using a pith-estimate indicator) that it likely germinated in the late 1500s which pre-dates the arrival of the region's first European explorer, Samuel de Champlain, in 1609 (National Park Service 2022). Consistent with their reported silvics (Burns and Honkala 1990), Eastern Red Cedar and Northern White

Table 7. Significant seasonal correlations of radial growth with deposition parameters (NO_3, SO_4 ,and pH) for 4 conifer and 4 hardwood species ($P \leq 0.05$) from 1937 to 2016. Years listed indicate the last year of a 10-year moving window for which correlations were conducted. Correlation coefficients (*r*) represent the highest or lowest *r* for a single year or span of years. ns indicates season with no significant correlations.

Species	NO_3	*r*	SO_4	*r*	pH	*r*
Northern White Cedar	1975–1977	-0.524				
	1987	0.697	1978–1986	-0.716	1978–1981	0.678
	2003–2004	-0.601	2016	0.598	2016	-0.712
Eastern Red Cedar			1979–1981	-0.603	1978–1982	0.808
			1983–1985	-0.734	1984–1985	0.665
	1979–1983	-0.807	1995	0.609	1995	-0.531
Eastern White Pine	2002	-0.610	1977–78	-0.651	1983–1985	0.648
	2008–2012	-0.776	2010–2012	-0.667	2010–2012	0.549
Eastern Hemlock	1982–1984	-0.828				
	2000–2002	-0.692	1978	-0.555	1982–1984	0.695
Northern Red Oak					2008–2009	0.513
	2008–2009	-0.602	2008	-0.473	2013–2016	-0.645
White Oak	2000	-0.662	ns		1982	0.715
American Beech	1982–1983	-0.810			1982	0.631
	2008–2009	-0.575	ns		1988	0.647
White Ash	1987	0.542				
	1988	-0.671				
	2000–2002	-0.806	ns		ns	

Cedar were the smallest and slowest growing trees evaluated, though they were the oldest species after White Oak and Eastern Hemlock. In fact, 1 Eastern Red Cedar had a tree ring originating in 1763, more than a decade before the American Revolution. The growth of Northern Red Oak somewhat exceeded the high levels reported for the species elsewhere in Vermont (Stern et al. 2020), while the growth of Eastern Hemlock mirrored reported levels, and growth of Eastern White Pine was somewhat below levels noted elsewhere in the state (Stern et al. 2021). Whereas the Stern et al. (2020, 2021) compiled data from many sites, dissimilarities of growth reported in those studies and our results at Red Rocks Park likely reflect site-specific differences in soils and other influences not measured for these studies. Though White Ash had fairly static, intermediate levels of growth for many years, recent increases in growth could reflect the effects of a release event caused by a significant ice storm in 1998. Although shade tolerant when young, White Ash trees become less shade tolerant with age and respond quickly to openings in the canopy (Burns and Honkala 1990). Although White Oak is generally regarded as a slow-growing species (Burns and Honkala 1990), in Red Rocks Park it showed modest and consistent growth that for years rivaled White Ash and always outperformed American Beech. The persistent, constrained growth of American Beech likely reflected chronic infection from beech bark disease (an insect–disease complex that reduces the woody growth of affected trees; Gavin and Peart 1993) that was visible on sampled trees.

Correlations of tree growth with environmental data

*Precipitation***.** Precipitation was the environmental parameter with the most numerous and longest cumulative duration of correlations with growth. Higher precipitation during many periods of the previous autumn and the winter, spring, and summer of ring formation were positively associated with growth for conifers and hardwoods. Even though precipitation has been increasing in the region during the past several decades (Clark and Crossett 2021, Janowiak et al. 2018), precipitation (as water and perhaps snow) may often be limiting within Red Rocks Park forests because the thin, rocky soils there likely limit the amount of water in the soil available to support photosynthesis and growth. This pattern is consistent with our hypothesis H_1. Positive correlations between growth and spring precipitation were particularly evident for coniferous species, especially Eastern White Pine and Eastern Hemlock. Access to available water would help support photosynthesis during spring, a pattern consistent with hypothesis H_4. Another pattern that was evident for both conifers and hardwoods was that precipitation in the spring and summer before and the autumn of ring formation was sometimes negatively associated with growth. Negative associations for the spring and summer prior to ring formation may reflect the noted phenomenon that high precipitation and growth one year often results in lower growth the next, presumably because if more carbohydrates are used for growth in a year, that leaves fewer stored reserves to fuel growth the next (e.g., Kosiba et al. 2017). Negative associations of growth with precipitation the fall of ring formation may reflect reduced photosynthetic gain used to fuel growth under conditions of increased rain and cloudiness (e.g., Stern et al. 2020). Positive correlations with winter precipitation were seen for all species at some point in their chronologies and may hint at the importance of water inputs during this period for recharging ground water to support later growth. However, considerable research with multiple species also suggests that it is snow that is especially important for promoting growth in cold environments.

*Snow***.** For both conifer and hardwood species, winter snowfall and snow duration were often positively associated with growth, a pattern consistent with hypothesis H_2. Detailed experimental analysis with *Acer saccharum* Marsh. (Sugar Maple) has shown that increased snowpack buffers soils from low temperature exposure and freezing, thereby safeguarding roots from freeze-induced injury that can then result in reduced aboveground growth (e.g., Comerford et al. 2013, Reinmann et al. 2019). Other growth/snow correlation analyses suggest that this may be broadly true for other species (e.g., *Betula alleghaniensis* Britton [Yellow Birch], American Beech, and to a lesser extent *Acer rubrum* L. [Red Maple]) within northern hardwood forests (Stern et al. 2022). Our data is the first to suggest that this may also be pertinent to additional hardwoods and conifers not previously evaluated in this way. Although not noted for other eastern North American conifers, reductions in growth and even ensuing mortality following low snowpack that allow for soil and root freezing are well documented for at least 1 western North American conifer: *Chamaecyparis nootkatensis* (D. Don) Spach (Yellow-cedar; e.g., Hennon et al. 2012, Schaberg et al. 2011). Snow may be a particularly necessary insulator at Red Rocks Park because soils are shallow there, so roots are likely more uniformly exposed to low temperatures that can result in freezing injury.

In contrast to the seemingly positive influence of snow in winter and for some hardwoods in spring, negative associations between snow and growth were mostly noted for conifers during the fall and spring shoulder seasons. Having greater snowfall or snow duration during fall or spring would be consistent with cold conditions that could limit shoulder-season photosynthesis and associated growth.

Temperature. Pervasive negative associations between Tmax and growth suggest wide-spread temperature sensitivities of species within and surrounding this limestone-bluff cedar–pine forest, which does not support our hypothesis of reduced heat stress in these lakeside forests [H_3]. Negative correlations with growth were especially evident for Tmax during the year of ring formation. As correlations with moisture featured so prominently overall, our observed negative temperature–growth correlations may point to a heat-associated drought signal. In an effort to prevent xylem cavitation during hot summer months, trees can reduce water loss by decreasing stomatal conductance, which limits uptake of carbon dioxide (Cowan and Farquhar 1977) and reduces photosynthesis and growth (Tyree and Cochard 1996). Throughout eastern North America, drought has been a prominent climate signal revealed in the tree rings among many diverse species (D'Orangeville et al. 2018, Martin-Benito and Pederson 2015). While higher temperatures drive a more moisture-limited environment, it is also possible that trees of the limestone bluff cedar–pine forest are sensitive to high temperature exposures more directly. Whereas photosynthetic levels increase, plateau, and then decline as temperatures rise, levels of respiration continually rise with temperature (Teskey et al. 2015). Heat-associated carbon losses when foliage experience elevated net respiration can deplete soluble carbohydrate pools that otherwise could fuel growth (Teskey et al. 2015).

A few exceptions to generally negative associations of temperature and growth were occasional time periods where Tmax was positively associated with growth for Northern White Cedar (spring), Eastern White Pine (pAutumn), and all 4 hardwood species (pSummer, pAutumn). For conifers, this could be a sign that higher temperatures help promote photosynthesis and growth at times when temperatures are generally cool [H_3]. Although not field verified for Northern White Cedar, it is well recognized that temperate conifers retain the capacity to photosynthesize outside of the traditional growing season when favorable environmental conditions exist, which occur more commonly during the shoulder seasons (e.g., Schaberg et al. 1995, 1998). However, it is curious that a suggestion of spring photosynthesis was noted for Northern White Cedar but not Eastern White Pine or Eastern Hemlock, species for which shoulder-season photosynthesis has been verified (Hadley and Schedlbauer 2002, Jurik et al. 1998). Perhaps there was something unique about the cliffside microsite at the south end of the park that favored early season carbon capture? For example, the southern and western orientations of these cliffside forests could provide greater sun exposure and foliar warming that promotes needle dehardening (Strimbeck and DeHayes 2000) and increases in photosynthetic capacity (Schaberg et al. 1998) earlier in the season than for conifers in more-interior forests. Among the hardwood species, positive associations of Tmax and growth were constrained to the year prior to ring formation, occurring mainly in the previous autumn for Northern Red Oak, White Oak, and American Beech. It is likely that higher autumn temperatures effectively lengthened the growing season thereby allowing for extended periods of carbon capture. Indeed, oak and beech species retain their leaves longer during autumn senescence compared to other hardwood counterparts due to the slow progression of abscission-layer formation (Abadia et al. 1996). This longer retention of leaves in autumn may be why a positive correlation between autumn temperatures and growth has been found for another Fagaceae species, *Castanea dentata* (Marsh.) Borkh. (American Chestnut; Schaberg et al. 2022).

Correlations of growth and Tmax for seasons the year prior to ring formation varied somewhat among the seasons and tree functional groups. Negative associations between previous spring Tmax and growth occurred more frequently for conifers. In contrast, previous year summer and autumn Tmax were often positively associated with growth the following year particularly for Eastern White Pine. This result suggests that, at least in some years, higher temperatures during summer and early fall may promote the production of soluble carbohydrates that can be stored to promote later growth.

Like Tmax, growth negatively associated with higher Tmin levels during the year of ring formation suggests a widespread temperature sensitivity of species within this limestone bluff cedar–pine forest, patterns that contrast expectations under hypothesis H_3. Once again, the noted exception to this pattern was Northern White Cedar, for which growth was positively associated with spring Tmin. In the year prior to ring formation, growth of Eastern White Pine (pSummer and pAutumn), Eastern Red Cedar (pSummer), Northern Red Oak (pAutumn), and White oak (pAutumn) exhibited limited positive correlations with Tmin. Negative associations of growth and Tmin the year prior to ring formation were more common for conifers, although American Beech also showed this pattern for certain years.

Pollution. Because the Red Rocks Park limestone bluff cedar–pine forest overlies calcium-rich bedrock at a low elevation that receives low inputs of pollution deposition (e.g., Mohnen 1992), and because this is comprised of species with little recorded sensitivity to acid deposition, we expected that trees here would show few signs of pollution impacts (H_5). Contrary to this expectation, negative associations of growth with nitrate or sulfate inputs and positive associations with precipitation pH were common for conifers during past periods of high pollution loading (prior to reductions mandated by the 1990 amendments to the Clean Air Act; Driscoll et al 2001, Kosiba et al. 2018). Acid deposition can leach calcium from soils and foliage resulting in calcium deficiencies that can predispose trees to damage and decline (e.g., Schaberg et al. 2001, 2010). Conifers are generally considered more vulnerable to calcium depletion because calcium-leaching loss through foliar cuticles can occur year-round (DeHayes et al. 1999). Although soils in Red Rocks Park are derived from calcium-rich limestone, the thin soils of the site may have constrained overall soil cation pools and contributed to reduced growth during the peak of acid deposition in past decades. Northern Red Oak was the hardwood species with the most apparent sensitivity to pollution inputs, though this correlation was quite limited. Other work has suggested that Northern Red Oak growth had at times been constrained by pollution exposure in Vermont back when pollution levels were higher (Stern et al. 2020).

Conclusion

Climate and pollution parameters correlated with growth for the cedars and pines characteristic to the limestone-bluff forest were similar to those noted for the other conifer and hardwood species evaluated. Increased precipitation either the autumn before or winter, spring, and summer the year of ring formation was positively associated with greater growth for all species. Snowfall and snow duration during winter were also correlated with higher growth for all species except White Oak. In general, higher temperatures (Tmax and Tmin, especially during the year of ring formation) were associated with reduced growth for both conifer and hardwood species. Negative correlations were particularly consistent and strong for temperatures during the year of ring formation in summer and fall, the seasons projected to display the greatest intensification of maximum temperatures in the Northeast in the future (Janowiak et al. 2018). Conifers showed stronger negative correlations with previous year temperatures, perhaps highlighting a greater sensitivity to high temperature stress. Conifers also showed greater negative associations to shoulder-season snowfall and snow duration the year before and during ring formation. These results suggests that cold/snowy autumns and springs may limit photosynthetic gain and growth for conifers which may rely on carbon capture during these seasons to remain competitive with hardwoods that generally have greater photosynthetic potential during the traditional growing season (e.g., Hadley et al. 2008). Only Northern White Cedar showed positive associations between spring temperature and growth during shoulder seasons, suggesting that physiological activity during this time may be particularly important to this component of the limestone bluff cedar–pine forest. These results highlight the broad moisture and temperature sensitivities of trees within and around this limestone cedar–pine forest situated at a shoreline location with great exposure to variable and sometimes extreme weather patterns, and with very thin soils that have low moisture-storage capacities. The sensitivities to contemporary temperature and precipitation levels that we documented may cause limestone bluff cedar–pine forests to be particularly vulnerable to warming and altered precipitation regimes projected for the Northeast and the Champlain Valley of Vermont (Janowiak et al. 2018). Furthermore, the greater periodicity and intensity of precipitation projected to accompany atmospheric warming could result in greater runoff, reduced soil infiltration, and longer gaps between rain events (Janowiak et al. 2018), increasing the likelihood of functional drought conditions within thin-soiled limestone bluff cedar–pine forests. On the upside, if pollution inputs continue to be low, pollution-associated constraints to growth should be minimal or non-existent moving forward. Already threatened by development and exotic species encroachment, alterations in weather regimes with climate change could put trees within and adjacent to these rare limestone bluff cedar–pine forests at even greater risk of decline and loss. To better sustain forests like the one we studied at Red Rocks Park, managers may want to prioritize control of invasive species because climate change is expected to increase stand disturbances (Janowiak et al. 2018) that favor intrusion of invasive species. In addition, climate change is projected to increase the suitable habitat of some species (e.g., Eastern Red Cedar, Northern Red Oak, and White Oak) that are either associated with or near limestone-bluff cedar–pine forests (Prasad et al. 2007–ongoing, Wilke et al. 2021). Whereas these species may require less managerial intervention, others (e.g., Northern White Cedar, Eastern White Pine, and Eastern Hemlock) that are projected to experience declines in suitable habitat (Prasad et al. 2007–ongoing, Wilke et al. 2021), may benefit from active management to sustain populations in these novel ecosystems as the climate shifts.

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