



## Phenology, cold injury and growth of American chestnut in a Range-Wide provenance test

Paul G. Schaberg<sup>a,\*</sup>, Paula F. Murakami<sup>b</sup>, Kendra M. Collins<sup>c</sup>, Christopher F. Hansen<sup>d</sup>, Gary J. Hawley<sup>e</sup>

<sup>a</sup> USDA Forest Service, Northern Research Station, 81 Carrigan Drive, Burlington, VT 05405, USA

<sup>b</sup> USDA Forest Service, Northern Research Station, 705 Spear Street, South Burlington, VT 05403, USA

<sup>c</sup> The American Chestnut Foundation, 705 Spear Street, South Burlington, VT 05403, USA

<sup>d</sup> University of Vermont, Rubenstein School of Environment and Natural Resources, 705 Spear Street, South Burlington, VT 05403, USA

<sup>e</sup> University of Vermont, Rubenstein School of Environment and Natural Resources, 81 Carrigan Drive, Burlington, VT 05405, USA

### ARTICLE INFO

#### Keywords:

Genetic sources  
Spring phenology  
Leaf and shoot freezing injury  
Temperature and moisture availability  
Tree rings

### ABSTRACT

The primary factor limiting the distribution and growth of American chestnut (*Castanea dentata* (Marsh.) Borkh.) in eastern North America is tolerance to chestnut blight that is caused by the introduced fungal pathogen *Cryphonectria parasitica* (Murr.) Barr. However, a better understanding of how genetics and the environment influence American chestnut physiology and growth will also be needed to guide restoration as blight-tolerant growing stock becomes available. Here we describe patterns of phenology, cold injury and radial growth for American chestnut from 13 seed sources that represent three temperature zones (warm, moderate and cold) grown together in a unique provenance test in Vermont, USA. Temperature zones were established using data on the mean minimum winter temperatures over 10–30 years for weather stations nearest seed source locations; these averages were  $-5\text{ }^{\circ}\text{C}$  and above for the warm temperature zone,  $-5$  to  $-10\text{ }^{\circ}\text{C}$  for the moderate temperature zone, and below  $-10\text{ }^{\circ}\text{C}$  for the cold temperature zone. There was a consistent trend for trees from the warm temperature zone to break bud and leaf out earlier, and experience greater spring leaf frost damage and shoot winter injury than trees from other temperature zones. After initial establishment, woody growth (approximately 6 years of ring counts) was robust and tended to be greatest among moderate temperature zone sources and lowest for cold zone sources. Especially for trees from the warm zone, earlier budbreak was associated with greater growth. Foliar frost injury was not associated with altered growth, whereas winter shoot damage was associated with lower growth – especially following significant shoot loss. Even though warm temperature zone sources experienced more winter injury than trees from cold temperature zones, the growth of cold temperature zone sources tended to underperform that for warm and moderate zone sources – this suggests that, at least for the limited time that we evaluated growth, greater protection from the cold may come at the cost of greater growth potential. Although American chestnut is considered to be a relatively drought-tolerant species and growth was assessed during a period of historically high precipitation, higher moisture availability the year before, and occasionally during, the year of ring formation was broadly associated with greater growth across the temperature zones. Despite the negative influences of winter shoot injury on growth, the overall productivity of trees was exceptional, even at the northern edge of the species' range provided that moisture availability was adequate.

### 1. Introduction

American chestnut (*Castanea dentata* (Marsh.) Borkh.) was once an important component of eastern United States (US) forests, with its range covering more than 800,000 km<sup>2</sup> (Braun, 1950; Jacobs, 2007)

from Maine to Georgia and west to the Ohio River valley (Little, 1977). American chestnut was especially prominent within the heart of this range where it was thought to represent 40% (Keever, 1953) to even 50% (Russell, 1987; Smith, 2000) of the forest canopy. American chestnut is fast-growing (diameter growth as great as 2.5 cm/yr;

\* Corresponding author.

E-mail address: [paul.schaberg@usda.gov](mailto:paul.schaberg@usda.gov) (P.G. Schaberg).

<https://doi.org/10.1016/j.foreco.2022.120178>

Received 27 December 2021; Received in revised form 14 March 2022; Accepted 18 March 2022

Available online 4 April 2022

0378-1127/Published by Elsevier B.V.

Buttrick, 1925; Kuhlman, 1978) and could achieve massive proportions (e.g., diameters of 1.5 m and heights of 37 m; Buttrick, 1925). Its wood is rot-resistant and straight-grained, qualities that historically rendered it suitable for a variety of uses including construction, woodworking, furniture, railroad ties, telephone poles, mine timbers and musical instruments (Anagnostakis, 1987). American chestnut can also produce abundant annual crops of nuts that were a nutritious food source for wildlife, domestic animals and humans (Rice et al., 1980).

In the early part of the twentieth century, chestnut blight (caused by the fungal pathogen *Cryphonectria parasitica* (Murr.) Barr) was introduced to the eastern US. The disease causes cankers that girdle and kill stems but leave root systems unharmed (Griffin, 2000). The stump sprouts that rise from undamaged tissues can persist for years, but resulting new stems typically succumb to the fungus before reaching reproductive maturity. As a consequence, an estimated three to four billion American chestnut trees were killed by blight in the first half of the last century, a process that functionally removed the species as an overstory tree within about 40 years of blight introduction (Anagnostakis, 1987; Griffin 2000). Because of American chestnut's once prominent ecological and economic value, many approaches to restore the species have been attempted (Beattie and Diller, 1954; Elliston, 1981; MacDonald and Fulbright, 1991; Newhouse et al., 2014). These include breeding efforts to provide blight tolerance through crossing American chestnut with Asian chestnuts (typically Chinese - *Castanea mollissima* Blume) that coevolved with the pathogen and show natural resistance to it (e.g., Anagnostakis, 1987), and through the insertion of genes from other species (e.g., oxalate oxidase from wheat; Newhouse et al., 2014; Westbrook et al., 2020) to help constrain fungal damage. Complimentary work is being conducted to breed stock tolerant of phytophthora root rot caused by the invasive microbe *Phytophthora cinnamomi* Rands, which limits American chestnut populations in southern portions of the species' range (Westbrook et al., 2019).

A critical aspect of restoring American chestnut to eastern forests is developing genetically diverse plants that are disease tolerant and locally adapted to the multitude of site conditions across the species' former range. For example, American chestnut once grew from USDA Plant Hardiness Zone 8a (with 30-year average annual minimum temperatures as low as  $-12.2^{\circ}\text{C}$ ) to zone 5a (30-year average annual minimum temperatures as low as  $-28.9^{\circ}\text{C}$ ) (USDA Agricultural Research Service, 2018). Considering this almost  $17^{\circ}\text{C}$  range in minimum temperature exposure and adaptation, matching hardiness levels of restoration stock to the hardiness zone of a planting site is likely important to prevent significant freezing injury that could limit tree productivity and vigor.

One way of assessing broad patterns of local or regional adaption, including relative sensitivities to environmental stresses such as potentially damaging low temperatures, is to measure the performance of trees in range-wide provenance tests (Wright, 1976). Here, trees from genetic sources from across a species' range are planted together in a common garden to evaluate how consistent or different plant performance is among genetic sources or groups of sources within regions. For example, through a synthesis of the results of many provenance tests for a range of tree species, Wright (1976) determined that, compared to northern sources, southern sources of the same species tend to grow faster, leaf out later in spring and are therefore less susceptible to spring leaf frost damage, and are more susceptible to winter cold damage. Although provenance tests have been a powerful tool for identifying patterns of traits that are important to tree productivity and survival, their application to American chestnut has been extremely limited because of the timing of steep population declines associated with chestnut blight relative to the advent and deployment of provenance plantings. Indeed, to our knowledge, the only range-wide provenance planting for American chestnut was started in 2009 on the Green Mountain National Forest in Vermont, USA (Saielli et al., 2014). This planting includes American chestnut from 13 seed sources ranging from North Carolina in the south to Maine and Vermont in the north.

Dagleish et al., (2016) contend that almost no information is available for American chestnut regarding the geographic variation of adaptive traits such as flushing date, thermal or moisture tolerances or growth rate. To remedy this deficiency, we used this unique Vermont planting to assess patterns of spring bud and leaf phenology, cold sensitivity and radial growth of chestnuts grouped by winter temperature zones (warm, moderate and cold), and to assess the influence of ambient temperature and moisture regimes on growth. A better understanding of how genetics and the environment modulate American chestnut physiology and growth is needed to guide breeding and management efforts, and inform the development of adaptive seed zones to help restore the species across the landscape once disease tolerance is achieved.

## 2. Materials and methods

### 2.1. Site description

Open-grown trees utilized in this study exist in a previously established common garden that was planted in June 2009 in Leicester, Vermont (latitude  $43^{\circ}50'37''\text{N}$ , longitude  $73^{\circ}02'01''\text{W}$ , elevation 348 m) and is within the boundaries of the Green Mountain National Forest (Saielli et al., 2014). These open grown trees were maintained in an mowed orchard setting that was one of three silvicultural treatments that also included a partial cut and a closed canopy control in the original Saielli et al. (2014) study. Open grown trees were the focus of the current study because canopy shading can significantly impact the various measurement parameters (e.g., cold exposure and injury, phenology and growth) that were evaluated here. This common garden is comprised of 13 open-pollinated American chestnut sources that correspond to much of the historic range of American chestnut from northerly Vermont to North Carolina in the south (Fig. 1). Each source represented one to three half-sib families. Here 12 trees from each of 13 sources were planted in a completely randomized design (total = 156 trees). At the time of the measurements described herein, only five trees had died since planting. Sources were grouped into three temperature zones based on their low temperature acclimation and elevation (Saielli et al., 2014) – warm (KY1, MD1, NJ1), moderate (NC1, NY1, NY2, PA1, PA2, VA1, VA2) and cold (ME1, ME2, VT1) (Fig. 1). These categories were established based on the mean minimum December, January and February temperatures over 10–30 years at weather stations nearest seed source locations (Saielli et al. 2014). These minimum temperature averages were  $-5^{\circ}\text{C}$  and above for the warm temperature zone,  $-5$  to  $-10^{\circ}\text{C}$  for the moderate temperature zone, and below  $10^{\circ}\text{C}$  for the cold temperature zone (Saielli et al. 2014).

### 2.2. Temperature data

Maximum and minimum temperatures were recorded every three hours in six locations within the plantation using iButton temperature loggers (model DS1922L, Embedded Data Systems, Lawrenceburg, KY). Data loggers were in sealed plastic bags that were fastened under open-ended, white plastic containers to prevent overheating when exposed to direct sunlight and minimize exposure to moisture. Temperature loggers were affixed to wooden stakes at approximately 70 cm above the ground. Data was downloaded twice a year (June following spring phenology and shoot winter injury assessments, and again in December) from 2010 to 2018. Field temperature data from mid-December 2016 to mid-June 2017 was unfortunately lost due to data logger failure and was supplemented by data from Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group, Oregon State University, 2020) for the purpose of statistical analyses. From temperature data we calculated monthly maximum (Tmax), average (Tave) and minimum (Tmin) temperatures (Fig. 2) as well as the temperature index growing degree days (GDD) from 2010 to 2018. GDD were calculated based on the accumulation of mean daily temperatures above a baseline of  $5^{\circ}\text{C}$  from January 1 until budbreak and leaf-out using the formula  $\text{GDD} =$

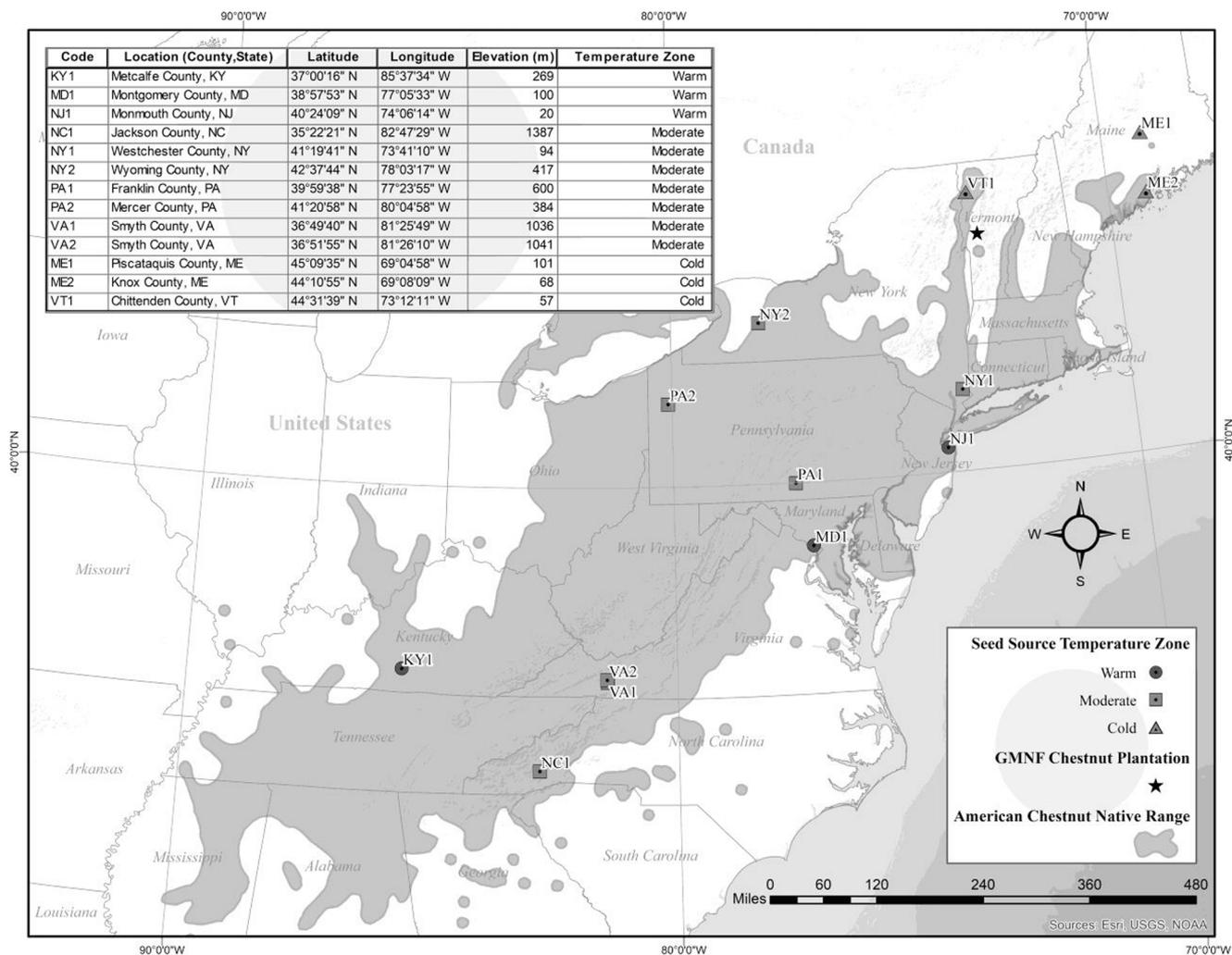


Fig. 1. Source codes, locations, latitudes, longitudes, elevations and temperature zones for the 13 open-pollinated American chestnut sources at the Green Mountain National Forest planting. Specific source data appears in the embedded Table and the spatial distribution of sources are depicted on the map. Each source represents one or two half-sib families, except for PA2, which was from three trees. American chestnut’s native range layer is from Little, 1977.

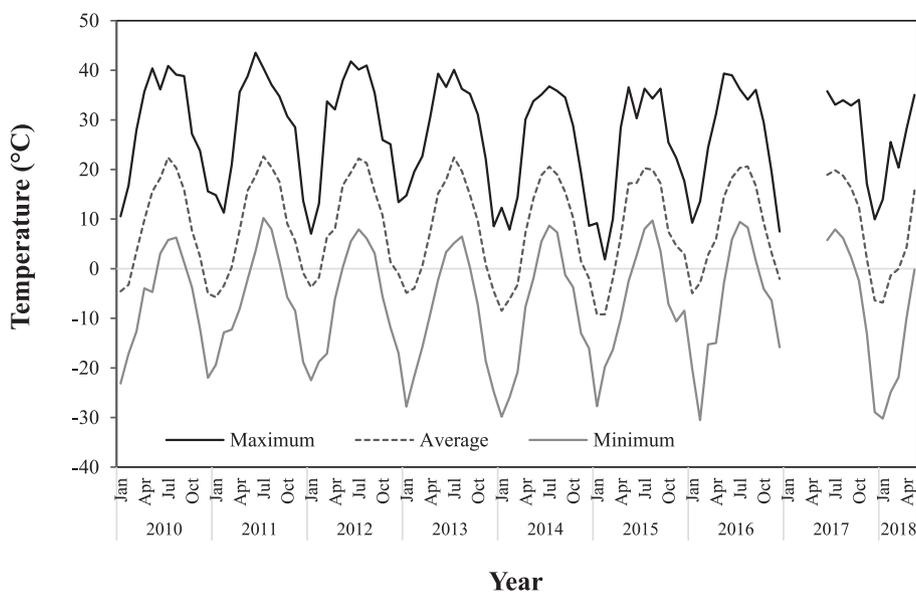


Fig. 2. Maximum, average and minimum air temperatures recorded in the American chestnut provenance planting in Leicester, Vermont from 2010 to 2018.

$\Sigma(T_m - 5 \text{ }^\circ\text{C}$  for  $T_m$  greater than  $5 \text{ }^\circ\text{C}$ ; 0 for  $T_m \leq 5 \text{ }^\circ\text{C}$ ), where  $T_m$  is the daily mean temperature. GDD is a measure of heat accumulation that is commonly used to predict phenological development in plants such as budbreak (e.g., Miller et al., 2001).

### 2.3. Phenology

Weekly assessments of spring budbreak and leaf-out were conducted for all trees beginning in April until leaves were fully expanded in mid-June from 2012 through 2016 using established protocols for American chestnut phenology (adapted from West and Wein, 1971) that rated bud development as 0 = bud dormant, no budbreak; 1 = bud displays a silver/green tip; 2 = bud green, but tight, no leaves unfolding; 3 = bud expanding, leaves unfolding; 4 = internodes visible, leaves hanging; 5 = internodes visible, leaves enlarged to complete elongation (see photographic depiction in Fig. S1). Individual trees received a phenological ranking that combined the rating for the most advanced terminal bud with an estimation of the total percent of buds at that rank to establish a final decimal rating. For example, a tree whose most advanced terminal bud was ranked 3 with 50% of the buds at this stage received a score of 3.5. The timing of leaf-out for each tree was determined using nonlinear curve fitting (JMP Pro 10 Statistics, SAS Institute, Inc., Cary, NC) as the number of days (Julian date) from January 1 to the estimated date when fifty percent or more of terminal buds reached rank 3.

### 2.4. Cold injury

During the five years of phenology assessment, our study site experienced three spring frost events from April 26–30, 2012, May 14–15, 2013 and May 23, 2015 in which temperatures fell below  $-2.0 \text{ }^\circ\text{C}$  and resulted in varying degrees of foliar injury to trees. We visually estimated and recorded the percent number of leaves exhibiting foliar frost damage relative to the whole tree in 5% increments. In addition, in 2013 and 2015 we assessed the percent re-flush of leaves (also in 5% increments) that occurred following these freeze events. Winter shoot freezing injury was also assessed for trees from 2012 through 2016 as a percentage of the number of current-year terminal shoots exhibiting visible dieback (shoot mortality evident as sunken portions of shoots that displayed dark coloration) relative to the estimated number of total terminal shoots. These shoot assessments took place in mid-June of each year after leaf-out to better distinguish new versus old shoot injury.

### 2.5. Dendrochronology

Increment cores were collected from 107 trees (27 from warm temperature zone sources, 54 from moderate temperature zone sources and 26 from cold temperature zone sources) using standard dendrochronological techniques (Stokes and Smiley, 1968) on October 30 and November 5, 2018. Two xylem increment cores (5 mm) were extracted from opposite sides of each tree at approximately 30 cm above the base of each tree. Coring at this height was necessary to avoid branching and allowed for a consistent place from which to extract cores from all trees. The diameter (cm) of each tree was measured at the site of increment core collection.

Cores were oven-dried, mounted on wooden blocks, and sanded with progressively finer grit sandpaper (ranging from 220 to 800). Visual crossdating of annual growth rings was performed using the list method (Yamaguchi, 1991) and microscopically measured to 0.001 mm precision using a Velmex sliding stage unit (Velmex Inc., Bloomfield, NY) and MeasureJ2X software (VoorTech Consulting, Holderness, NH). Because American chestnut is a ring-porous species, in addition to whole ring width we also measured earlywood width (EWW) and latewood width (LWW). Cores were visually crossdated and then the program COFECHA was used to statistically detect crossdating errors (Holmes, 1983; Grissino-Mayer, 2001). Whole ring width (WRW) measurements were averaged per tree and used to calculate basal area increment (BAI ( $\text{cm}^2$ /

year); function `bai.out`, R package `dpLR`; Bunn et al., 2016) thereby adjusting for size related growth trends (West, 1980).

For comparisons of growth with temperature and moisture data, whole ring widths were averaged per tree, detrended, standardized and prewhitened (functions `detrend` and `chron`, R package `dpLR`; Bunn et al., 2016). We chose a 67%  $n$  cubic smoothing spline for detrending since it has the benefit of minimizing growth trends considered noise while maintaining existing climate signals in the chronology (Cook and Peters, 1981). The resulting standardized individual tree chronologies were then used to create a stand-wide residual chronology with a Tukey's biweight robust mean to produce ring width index (RWI) chronologies used to test relationships with climate data.

### 2.6. Statistical analyses

Yearly differences in the timing (Julian days and GDD) of budbreak and leaf-out, foliar frost damage, post-frost foliar re-flush, shoot winter injury, EWW, LWW, and BAI growth among sources in the three temperature zones were determined by repeated measures analyses of variance followed by Tukey-Kramer HSD post-hoc tests to evaluate specific differences among temperature zones when variances among groups were equal. When they were not, the Steele-Dwass test for unequal variances was used to evaluate differences associated with temperature zone. All tests were conducted using JMP Pro 10 statistical software (SAS Institute, Inc., Cary, NC) and were considered statistically significant if  $P \leq 0.05$ . Our focus was to evaluate measurement parameter differences among the temperature zones because broad and consistent differences at this scale are more likely to inform breeding and transplant decisions important to regional restoration efforts. Information on differences in response (mean  $\pm$  SE) among seed sources within temperature zones appear in supplementary tables (Tables S1–S5).

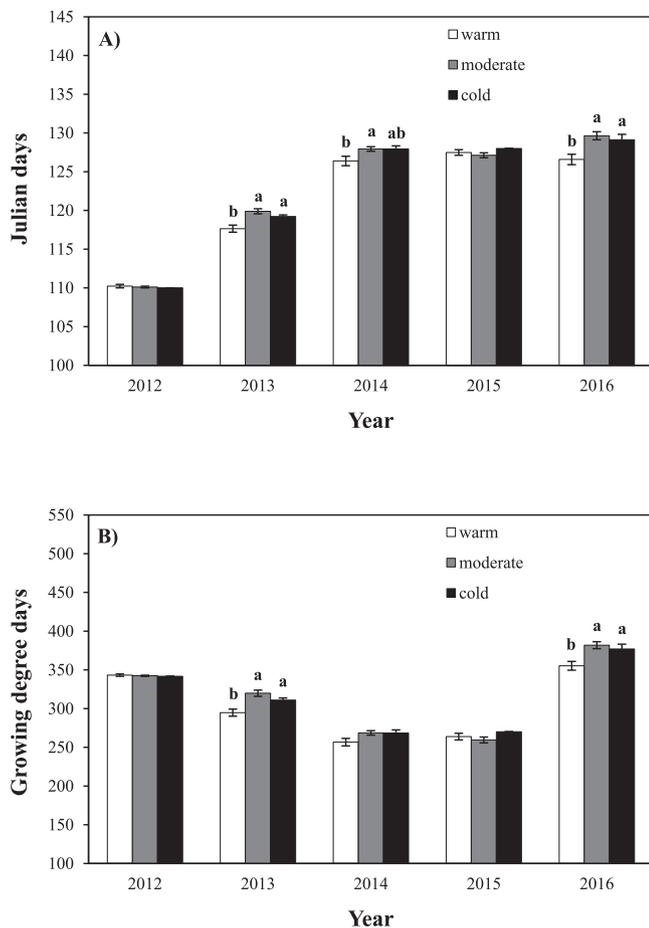
RWI chronologies were utilized to relate stand-wide growth with monthly temperature and moisture metrics from the previous year's growing season beginning in April (months represented by lower case letters, i.e., apr to dec) to the end of the current year growing season (months represented by upper case letters, i.e., JAN to SEP) using Pearson's correlations (function `dcc`, R package, `treeclim`; Zhang and Bondi, 2015).

Relationships between temperature and growth were conducted using calculations of monthly  $T_{max}$ ,  $T_{ave}$  and  $T_{min}$  obtained from field data loggers. Monthly growing degree days (GDDm) were calculated using the R package `pollen` (function `gdd`; Nowosad, 2018) with a base temperature of  $5 \text{ }^\circ\text{C}$ . Relationships between moisture and growth included location-specific data obtained from the Standardized Precipitation-Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2017). We used two time-steps in our analyses to ascertain the possible influence of moisture data specific to single months (SPEI01) and groups of 3 consecutive months (SPEI03). SPEI01 was used to detect individual months of potential importance to growth, whereas SPEI03 was used to test for relationships on a seasonal basis. In addition, we compared stand-wide growth to water year precipitation (Wry, a measure of total precipitation beginning October 1 of the previous year to September 30 of the current year) obtained for Addison County, Vermont (NOAA National Centers for Environmental Information, 2020) to determine the impact of accumulated moisture (in the form of precipitation and snowmelt) on growth.

## 3. Results

### 3.1. Phenology and cold injury

Budbreak started as early as Julian day 110 (April 20 in 2012) and as late as day 129 (May 9 in 2016) – a 19 day spread in response (Fig. 3). Differences in the timing of budbreak among seed source temperature zones varied among the years. However, when significant differences



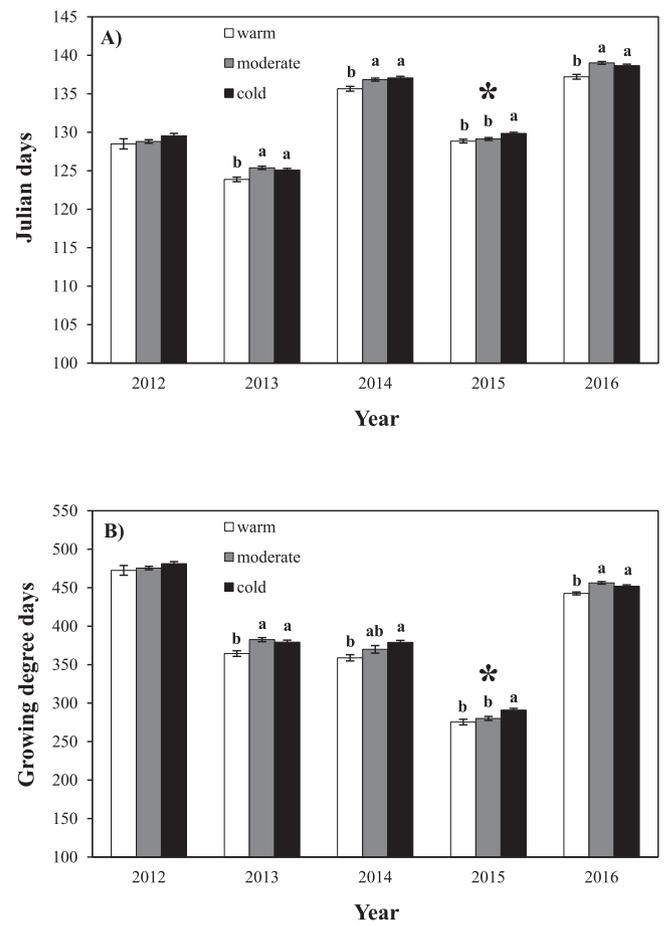
**Fig. 3.** Julian days (A) and growing degree days (GDD) (B) to budbreak among warm (white), moderate (gray) and cold (black) seed source temperature zones of *Castanea dentata* growing in common garden in Leicester, Vermont. Means ( $\pm$ SE) within a year with different lowercase letters are significantly different based on Tukey-Kramer HSD tests ( $P \leq 0.05$ ).

among temperature zones were found, sources from the warm temperature zone generally broke bud earlier than sources from the other temperature zones. Although also variable, sources from the warm temperature zone tended to break bud following exposure to fewer GDD.

Leaf-out started as early as Julian day 123 (May 3 in 2013) and as late as day 139 (May 19 in 2016) – a 16 day spread in response (Fig. 4). Differences in leaf-out among seed source temperature zones varied somewhat among the years, though showed greater consistency in response than budbreak. Like budbreak, seed sources from the warm temperature zone tended to leaf-out earlier than the other temperature zones. Also similar to budbreak, warm temperature zone sources tended to leaf-out following exposure to fewer GDD.

Spring frost damage to emerging leaves was detected in three years of our study and ranged from mild (2012 with < 33% of leaves) to severe (2015 with 100% of leaves showing damage) (Fig. 5). Differences in frost injury among temperature zone sources were only detected in years of mild or moderate injury, when either sources in the warm temperature zone (2012) or warm and cold temperature zone sources (2013) experienced greater injury. Temperature zone-related differences in leaf re-flush following frost injury were evident in the two years of high injury; in 2013 sources from the moderate temperature zone had the least re-flush, and in 2015 sources from the warm temperature zone had the least re-flush. The higher re-flush in 2015 followed the uniformly high foliar frost injury recorded that year.

Shoot winter injury was evident every year, though levels ranged from low (an average of < 5% of shoots) to high (an average of about



**Fig. 4.** Julian days (A) and growing degree days (GDD) (B) to leaf-out among warm (white), moderate (gray) and cold (black) seed source temperature zones of *Castanea dentata* growing in common garden in Leicester, Vermont. Means ( $\pm$ SE) within a year with different lowercase letters are significantly different based on Tukey-Kramer HSD tests ( $P \leq 0.05$ ) except where indicated by an asterisk when non-parametric Steele-Dwass tests were performed.

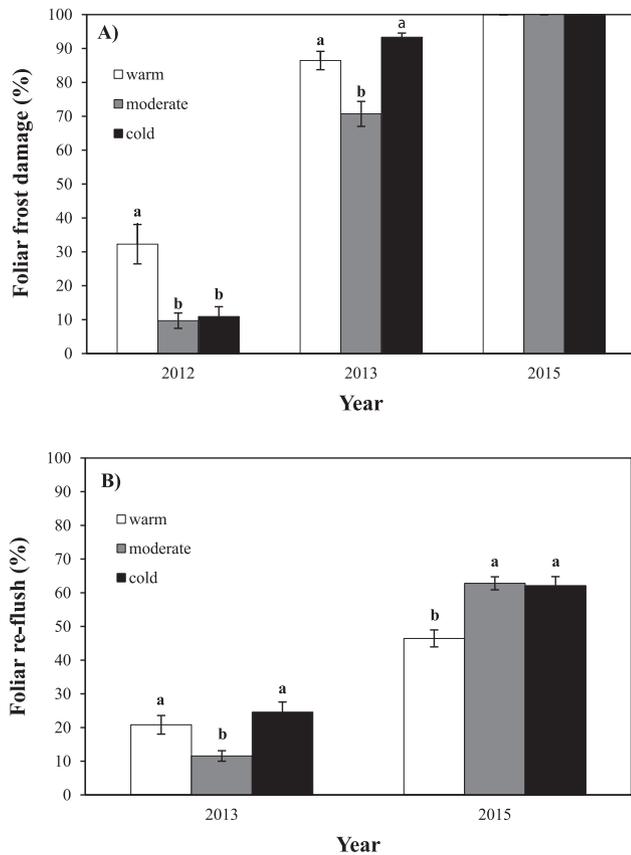
40% of shoots) (Fig. 6). In three of the five years assessed, sources from the warm temperature zone experienced significantly greater shoot freezing injury.

### 3.2. Radial growth

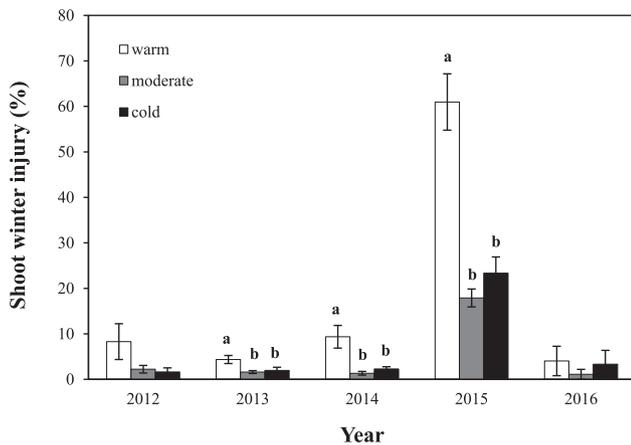
The EWW growth gradually increased for the first four years, but then reached a fairly stable and higher level by 2015 (Fig. 7A). Differences in EWW growth among temperature zone sources were detected in three of the last four years assessed. Though specific differences varied over time, there was a tendency for growth to be greatest among moderate temperature zone sources and least for warm temperature zone sources. LWW growth also trended upward over time, but significant differences among temperature zone sources were limited to 2012 and 2013 (Fig. 7B). During these years cold temperature zone sources generally experienced lower LWW growth. BAI also trended upward over time and reached an average of over 30 cm<sup>2</sup> in 2018 (Fig. 7C). Differences in BAI growth among temperature zone sources were detected before 2016 when overall growth was low. During this time, growth was generally lowest for cold temperature zone sources.

### 3.3. Associations of growth with phenology, cold injury and climate data

For all temperature zones combined, earlier leaf-out and lower GDD were associated with higher growth in three of the five years assessed

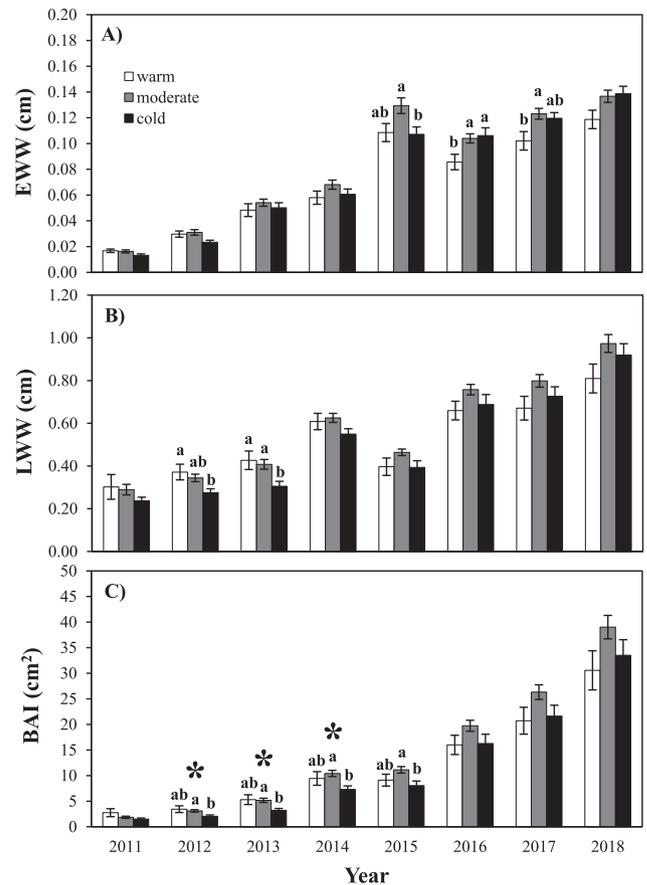


**Fig. 5.** Foliar frost damage (A) and foliar re-flush (B) among warm (white), moderate (gray) and cold (black) seed source temperature zones of *Castanea dentata* growing in common garden in Leicester, Vermont. Means ( $\pm$ SE) within a year with different lowercase letters are significantly different based on Tukey-Kramer HSD tests ( $P \leq 0.05$ ).



**Fig. 6.** Shoot winter injury among warm (white), moderate (gray) and cold (black) seed source temperature zones of *Castanea dentata* growing in common garden in Leicester, Vermont. Means ( $\pm$ SE) within a year with different lowercase letters are significantly different based on Tukey-Kramer HSD tests ( $P \leq 0.05$ ).

(Table 1). This negative association was also detected for EWW in 2014. Negative associations between shoot winter injury and growth were also seen in 2014 and especially 2015 – the year of greatest winter shoot damage. Warm temperature zone sources had significant relationships between all growth metrics (BAI, EWW and LWW) and spring phenology measures (Julian date and GDD) in 2013 and 2015, whereas moderate



**Fig. 7.** Earlywood width (EWW) (A), latewood width (LWW) (B) and basal area increment (BAI) (C) among warm (white), moderate (gray) and cold (black) seed source temperature zones of *Castanea dentata* growing in common garden in Leicester, Vermont. Means ( $\pm$ SE) within a year with different lowercase letters are significantly different based on Tukey-Kramer HSD tests ( $P \leq 0.05$ ) except where indicated by an asterisk when non-parametric Steele-Dwasse tests were performed.

and cold temperature zone sources had none (Table 2). For warm temperature zone sources, LWW (in 2012 and 2015) and BAI growth (2015) were negatively associated with shoot winter injury. Foliar frost injury was negatively associated with EWW growth for warm sources in 2012 and LWW for cold sources in 2012 and 2013. Growth was negatively associated with foliar re-flush among moderate (BAI and LWW) and cold (LWW) temperature zone sources in 2013, but LWW was positively related to foliar re-flush among warm sources in 2015.

American chestnut radial growth had far more significant relationships with moisture data (Fig. 8) than temperature measures (Fig. 9). For trees from all three temperature zones there was a consistent pattern for moisture metrics for months prior to the current growing season to be positively associated with growth (RWI; Fig. 8), with many of the associated correlation coefficients being quite high. In addition, and only for the warm temperature zone sources, there were negative correlations for moisture in the previous October and December with growth the following year. Another divergence among general patterns was that, for only moderate temperature zone sources, growth was positively associated with moisture during the spring of ring formation. In contrast, associations between temperature and growth were consistent for all three temperature zones; growth was negatively correlated with temperature in one time period – the previous December’s average and minimum air temperatures.

**Table 1**

Linear regressions comparing basal area increment (BAI), earlywood width (EWW) and latewood width (LWW) of all trees to shoot winter injury, number of Julian days to leaf-out, growing degree days (GDD) to leaf-out (base temp = 5 °C), foliar frost damage and foliar re-flush. Significant relationships ( $P \leq 0.05$ ) are represented by their corresponding coefficients of determination ( $r^2$ ) while non-significant relationships are represented by “ns”. An “x” denotes where regression analysis was not possible. Parenthetical symbols below coefficients of determination indicate whether relationships were positive (+) or negative (-).

Year	Growth parameter	n	Shoot winter injury	Julian days to leaf-out	GDD	Foliar frost damage	Foliar re-flush
2012	BAI	73	ns	0.075 (-)	0.066 (-)	ns	x
	EWW		ns	ns	ns	ns	x
	LWW		ns	0.085 (-)	0.079 (-)	ns	x
2013	BAI	84	ns	ns	ns	ns	0.135 (-)
	EWW		ns	ns	ns	ns	ns
	LWW		ns	ns	ns	ns	0.145 (-)
2014	BAI	98	ns	0.045 (-)	0.058 (-)	x	x
	EWW		0.052 (-)	ns	ns	x	x
	LWW		ns	0.041 (-)	0.047 (-)	x	x
2015	BAI	104	0.089 (-)	0.075 (-)	0.082 (-)	ns	ns
	EWW		0.067 (-)	0.061 (-)	0.065 (-)	ns	ns
	LWW		0.181 (-)	0.039 (-)	0.042 (-)	ns	0.039 (+)
2016	BAI	107	ns	ns	ns	x	x
	EWW		ns	ns	ns	x	x
	LWW		ns	ns	ns	x	x

**Table 2**

Linear regressions comparing earlywood width (EWW), latewood width (LWW) and basal area increment (BAI) of warm, moderate and cold temperature zone sources to shoot winter injury, number of Julian days to leaf-out, growing degree days (GDD) to leaf-out (base temp = 5 °C), foliar frost damage and foliar re-flush. Significant relationships ( $P \leq 0.05$ ) are represented by their corresponding coefficients of determination ( $r^2$ ) while non-significant relationships are represented by “ns”. An “x” denotes where regression analysis was not possible. Parenthetical symbols below coefficients indicate whether relationships were positive (+) or negative (-).

Year	Temperate zone	n	Growth parameter	Shoot winter injury	Julian days to leaf-out	GDD	Foliar frost damage	Foliar re-flush	
2012	warm	14	EWW	ns	ns	ns	0.474 (-)	x	
			LWW	0.309 (-)	ns	ns	ns	x	
	moderate	84	all	ns	ns	ns	ns	x	
			cold	18	EWW	ns	0.398 (-)	0.318 (-)	ns
				LWW	ns	ns	ns	0.235 (-)	x
2013	warm	18	BAI	ns	0.279 (-)	0.311 (-)	ns	ns	
			EWW	ns	0.293 (-)	0.287 (-)	ns	ns	
			LWW	ns	0.229 (-)	0.272 (-)	ns	ns	
	moderate	45	BAI	ns	ns	ns	ns	0.143 (-)	
			LWW	ns	ns	ns	ns	0.106 (-)	
	cold	21	LWW	ns	ns	ns	0.230 (-)	0.261 (-)	
2014	warm	23	all	ns	ns	ns	x	x	
	moderate	50	all	ns	ns	ns	x	x	
	cold	25	all	ns	ns	ns	x	x	
2015	warm	26	BAI	0.188 (-)	0.183 (-)	0.210 (-)	ns	ns	
			EWW	ns	0.163 (-)	0.190 (-)	ns	ns	
			LWW	0.338 (-)	0.165 (-)	0.174 (-)	ns	0.198 (+)	
	moderate	52	all	ns	ns	ns	ns	ns	
			cold	26	all	ns	ns	ns	ns
	2016	warm	27	all	ns	ns	ns	x	x
moderate		54	all	ns	ns	ns	x	x	
	cold	26	all	ns	ns	ns	x	x	

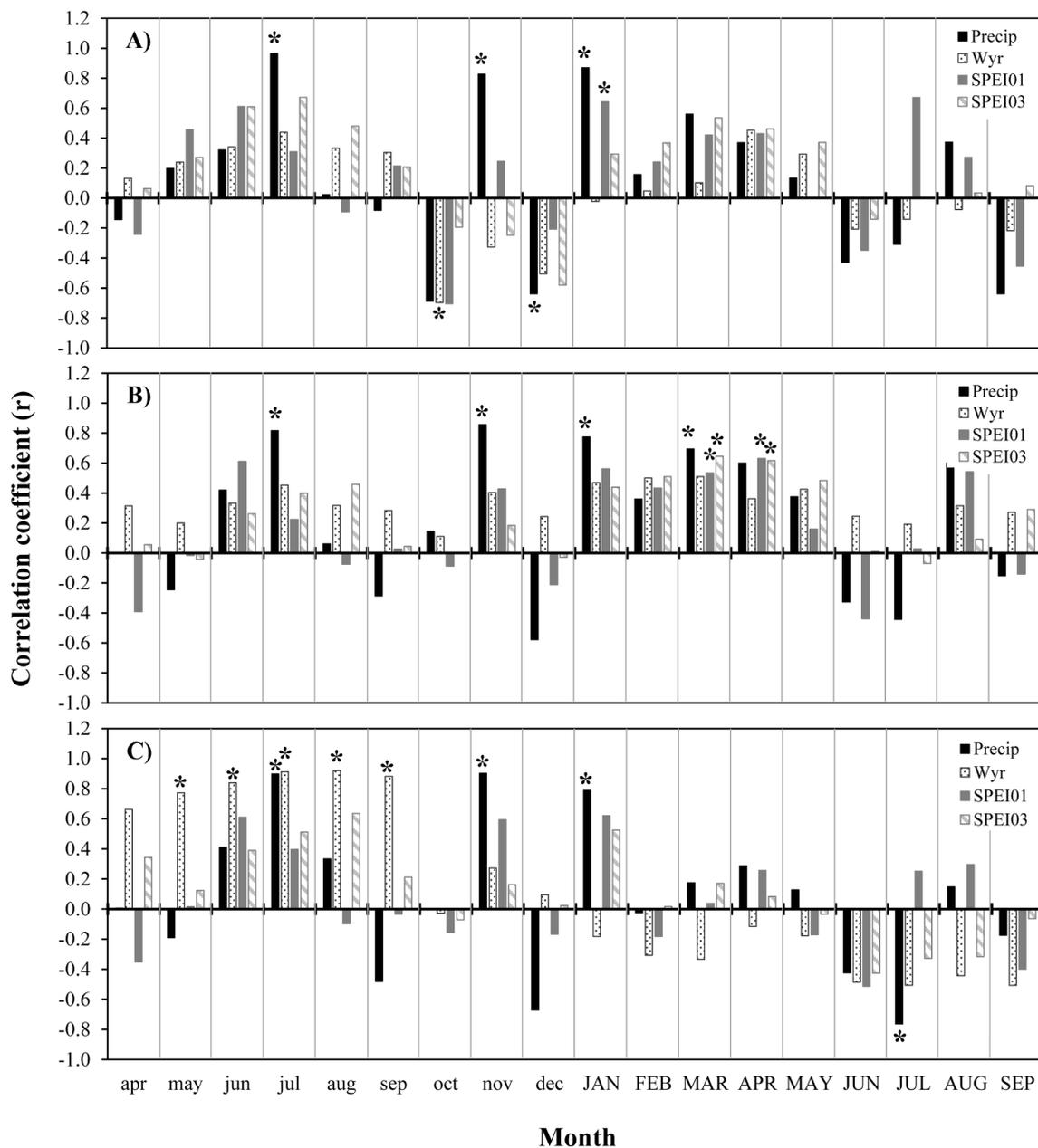


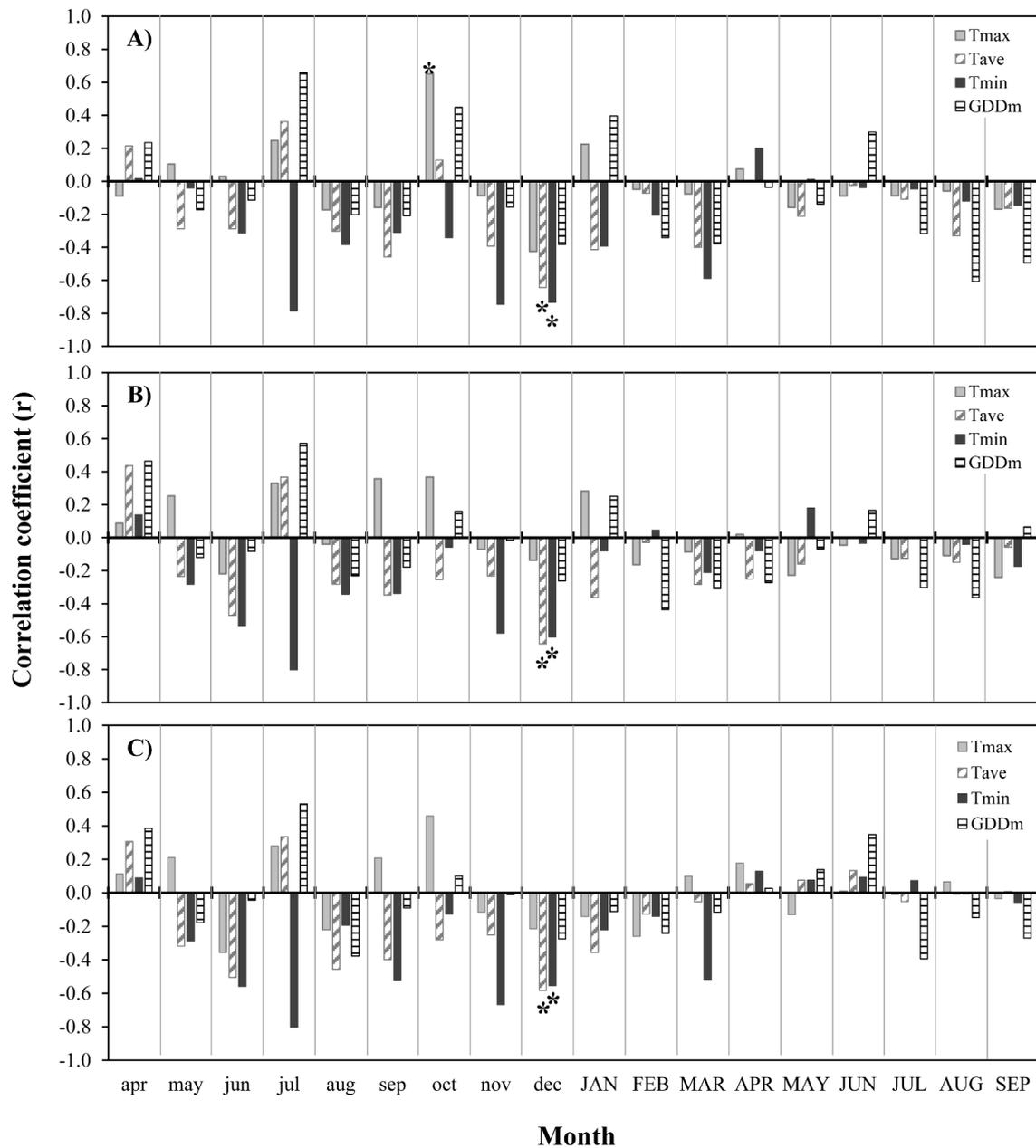
Fig. 8. Correlation coefficients (r) for moisture metrics and growth (RWI) for (A) warm temperature zone sources, (B) moderate temperature zone sources, and (C) cold temperature zone sources. Significant correlations are indicated by a \* ( $P \leq 0.05$ ).

## 4. Discussion

### 4.1. Phenology and cold injury

The broad range in Julian date and GDD associated with budbreak and leaf-out provides evidence of the great phenological plasticity of American chestnut. Despite this plasticity, there was a consistent trend for seed sources from the warm temperature zone to break bud and leaf out earlier. This trend in earlier leaf expansion was at times associated with greater spring frost injury if low temperature exposure coincided with leaves being more expanded and vulnerable to damage from early frosts (e.g., warm sources in 2012). However, injury in the field appeared to be an integration of the timing and speed of leaf expansion (that influence the vulnerability of tissues) and the timing and degree of low temperature exposure. For example, despite some variation in the timing of leaf-out, in 2015 leaves from all temperature zone sources experienced uniformly high damage to leaves following a region-wide

late season frost event. Frost damage to developing foliage of other species (e.g., *Acer saccharum* Marsh and *Acer rubrum* L.) was also widespread in Vermont that year, and was mapped at over 9,858 ha during aerial surveys that followed a freeze event on May 22 (Vermont Agency of Natural Resources Department of Forest Parks and Recreation, 2015). The trends that we found for warm temperature zone sources to leaf-out earlier and occasionally experience greater spring frost damage was opposite the general patterns that Wright (1976) noted in a multi-species summary of provenance trial results. However, a noted exception to overall trends in phenology was shown for another ring-porous hardwood – black walnut (*Juglans nigra* L.). For this species, southern sources started spring growth 5–10 days earlier and were often more sensitive to damage from late frosts than northern sources (Wright, 1976). A divergent pattern of response is consistent with evidence that ring-porous species experience later leaf-out because they first grow earlywood vessels that then supply water for subsequent leaf expansion (see discussion of EEW in 4.2 Radial growth). Other work has shown that



**Fig. 9.** Correlation coefficients (r) for temperature metrics and growth (RWI) for (A) warm temperature zone sources, (B) moderate temperature zone sources, and (C) cold temperature zone sources. Significant correlations are indicated by a \* ( $P \leq 0.05$ ).

the earlier onset of vessel formation in ring porous versus diffuse porous species is a generalized phenomenon (e.g., Suzuki and Suzuki 1996; Takahashi et al. 2015).

Shoot winter injury also varied greatly among years and seed source temperature zones. In general, shoot winter injury was low, with typically <10% of shoots showing tip mortality. However, in 2015 about 20% of shoots from moderate and cold temperature zone sources and over 60% of shoots from warm zone sources experienced freezing injury. This tendency for greater winter injury among warm temperature zone sources was evident in most years, and is consistent with results for numerous species (Wright, 1976). This tendency also highlights the importance of matching the cold tolerances of planting stock to the temperature norms of the planting site (e.g., by employing USDA Plant Hardiness Zone guidelines; USDA Agricultural Research Service, 2018).

#### 4.2. Radial growth

Changes in BAI over time show the progression of growth from modest increments when plant material was becoming established, to the increased growth of pole-sized trees. Indeed, average overall BAI in 2018 was approximately 34 cm<sup>2</sup>. However great, there is no reason to suspect that growth in 2018 represented the maximum growth for these trees because 1) BAI showed no signs of plateauing (Fig. 7C), and 2) linear growth in 2018 (1.052 cm) was less than half of the 2.5 cm/year reported for the species elsewhere (e.g., Buttrick 1925, Kuhlman 1978). Growth was expected to be high because trees were open grown and young. Although not directly comparable, this growth far exceeded the maximum growth reported for mature, dominant and co-dominant northern hardwood species within Vermont forests (e.g., *Acer saccharum* (17.7 cm<sup>2</sup>), *Acer rubrum* (18.5 cm<sup>2</sup>), *Betula alleghaniensis* Britton (17.3 cm<sup>2</sup>) and *Fagus grandifolia* Ehrh. (16.2 cm<sup>2</sup>); Stern, 2019). American chestnut growth in 2018 also exceeded the maximum growth

reported for mature *Quercus rubra* L. (26.2 cm<sup>2</sup>; Stern et al., 2020) and *Tsuga canadensis* (L.) Carrière (26.2 cm<sup>2</sup>) trees in Vermont, though it was somewhat less than that noted for mature *Pinus strobus* L. (40.7 cm<sup>2</sup>) (Stern et al., 2021). Growth levels in 2018 are consistent with historical (Buttrick, 1925) and recent evidence that American chestnut is an extremely fast-growing species with productivity levels that can far exceed co-occurring species (Jacobs and Severeid 2004, Wang et al., 2013, Belair et al., 2014). For example, McEwan et al. (2006) noted that American chestnuts released following harvest could experience growth that was nearly double that of associated hardwoods.

Differences in BAI among the temperature zone sources were small and limited to the period of planting establishment. When differences did exist, there was a tendency for trees from the cold temperature zone to grow less than trees from warm and moderate zones. In general, results from other provenance tests for a range of tree species consistently indicate that trees from more northerly populations generally grow more slowly but achieve greater cold hardiness than sources from southern populations (Wright, 1976). It has been theorized that plants can encounter an ecological tradeoff between diverting energy and resources toward growth versus the formation of protective compounds (Herns and Mattson, 1992). Evidence of this tradeoff relative to growth and cold tolerance has been documented via provenance studies for a broad range of tree species (Wright, 1976). More specifically, signs of this tradeoff were evident within the planting studied here based on measurements of first year of height growth and shoot winter injury (Saielli et al., 2014). In the current study, cold temperature zone sources often had lower BAI and LWW growth during establishment, but also experienced less shoot winter injury. Perhaps especially when plants are smaller and total carbon stores are modest, species like American chestnut that have hardiness levels that are marginal relative to ambient temperature lows (Gurney et al., 2011) are more likely to be impacted by a tradeoff in resource allocation towards growth versus protection.

Like BAI, differences in LWW among temperature zone sources were limited to the establishment period, with a tendency for lower LWW growth among cold zone sources relative to others. In contrast to BAI and LWW, differences in EWW occurred in later years when there was a tendency for EWW growth to be lowest among warm temperature zone sources. In temperate ring-porous trees, early wood vessels begin growth before budbreak to provide water conduction and associated turgor pressure needed for leaf expansion (Kudo et al., 2015). Although the warm temperature zone sources did break bud and experience leaf elongation earlier in the year than the other sources, temperatures during this earlier period were lower and less conducive to optimal growth (Fig. 2), which perhaps contributed to reduced EWW growth in some years.

#### 4.3. Associations of growth with phenology and cold injury

The strongest and most consistent relationships among foliar and shoot metrics and growth involved associations with spring budbreak and leaf-out (Table 1). Especially for trees from warm temperature zone sources that tended to break bud and leaf out first, there were significant negative relationships between EWW, LWW and BAI growth with Julian days and GDD in two of the five years assessed (Table 2). Relationships between phenological metrics and growth were consistent with the possibility that earlier leaf development functionally lengthens the growing season and can result in increased woody growth. Growth was also negatively associated with shoot winter injury, especially in 2015 – the year with the greatest freezing injury. This suggests that, at least when winter shoot mortality is high, that associated reductions in photosynthetic area and stored nonstructural carbohydrates can deplete carbon sources used to fuel growth. Even with reductions in growth following winter injury, trees steadily increased in growth following the 2015 winter injury event, and exhibited robust growth by 2018.

Foliar frost damage was not associated with changes in growth, and foliar re-flush following spring frost injury had an inconsistent

relationship with growth across the years. Higher foliar re-flush was associated with reduced BAI and LWW growth in 2013 when frost injury was high (83% on average) but re-flush levels were only modest (19% on average). In contrast, higher re-flush was associated with increased LWW in 2015 when frost damage was very great (100% of leaves with at least some injury for trees from all temperature zones) and re-flush was also considerable (57% on average, but somewhat lower for warm temperature zone sources). These results are consistent with the possibility that improved growth following foliar damage is possible provided that significant crown recovery allows for associated photosynthetic gains.

#### 4.4. Associations of growth and climate data

The most prominent associations between climate parameters and growth involved moisture metrics (Fig. 8). In general, for all three temperature zone sources, higher moisture availability in the summer, late fall and mid-winter before the spring of woody growth were all significantly associated with greater xylem productivity. Correlations with moisture metrics for the previous growing season highlight the importance of stored non-structural carbohydrates in fueling growth the following year. Stored carbon reserves are used to construct EW vessels that are initiated before budbreak (e.g., Kudo et al., 2015). Indeed, the importance of moisture availability to growth is expected for species adapted to conduct large volumes of water through its EW vessels (Zimmerman, 1983). For moderate temperature zone sources, the correlation between March and April moisture metrics and growth in the same year are unlikely to be associated with changes in stored carbohydrates because these stores would not be added to during the leafless period. However, this association could be related to the availability of water needed to provide the turgor pressure that helps growing xylem cells expand (Kudo et al., 2015). Although detected for sources from all three temperature zones, an explanation for associations between growth and previous November and current January moisture metrics (a time when trees are leafless so no carbon gains or cell division occur) is less intuitive, but could involve early snowpack development. Snow acts as a potent insulator of forest soils, buffering them from low air temperatures that can lead to soil freezing and root freezing injury that can then reduce aboveground growth (Comerford et al., 2013; Reinmann et al., 2018). However, the possible influence of snowpack on growth is less convincing for warm temperature zone sources which, in addition to showing positive associations between growth and November and January moisture levels, also showed negative associations with moisture in the adjacent months of October and December. Regardless of the exact time of water availability, the only other study to report climate-growth relationships for American chestnut also emphasized the importance of adequate moisture in fueling growth; increased growth was associated with increased precipitation and decreased Palmer Drought Severity Index (McEwan et al., 2006).

#### 4.5. Implications for future restoration in northern latitudes

American chestnut is considered to be a relatively drought-tolerant species (Wang et al., 2013). Our study was conducted during a period of historically high precipitation (Pederson et al., 2013), and the Northeast is expected to experience increases in both temperature and precipitation throughout the 21st century (Janowiak et al., 2018). However, increased evapotranspiration coincident with higher temperatures can create drought conditions, even in areas like the Northeast that are projected to experience increased moisture (Cook et al., 2014). The strong positive associations we found between moisture availability and growth suggest that American chestnut could be well poised to prosper under conditions of high evaporative demand provided that water recharge opportunities also exist. American chestnut is a deep-rooted, ring porous species that is particularly well-suited for acquiring and efficiently transporting water and maintaining the leaf

water potentials needed to maximize photosynthesis and growth (Wang et al., 2013). Furthermore, our Vermont plantation is at the northern edge of American chestnut's historical range where low temperatures have likely constrained optimal performance (Saielli et al., 2014). As such, plantings like ours could actually benefit from modest temperature increases, especially if they increase the functional growing season by accelerating spring budbreak and leaf-out, and reduce the likelihood of spring leaf frost and winter shoot injury – all factors documented as being relevant here.

The nature and scale of our study (which used yearly measures of growth for trees from varied genetic sources planted in one location) is not directly comparable to those used by the Climate Change Tree Atlas (CCTA; which uses periodically collected forest inventory data for trees across a species' range), so differences between growth and climate associations obtained using these divergent approaches were expected. Nonetheless, consistent with our findings, two of the top three predictors of suitable habitat for American chestnut in the CCTA are measures of precipitation (annual and mean May-September; Prasad et al., 2007-ongoing). However, inconsistent with our results, the CCTA counts four temperature measures among the top 10 predictors of American chestnut suitable habitat – mean annual, mean July, mean May-September and mean January temperature (Prasad et al., 2007-ongoing). We found that American chestnut growth was significantly associated with temperatures for only one period – the December prior to annual growth (Fig. 9). This negative relationship suggested that either high temperatures in December resulted in lower growth the following year or that low temperatures during December were related to improved growth the following year. The first possibility could reflect increased respiration during warm Decembers that could diminish stored non-structural carbohydrates that otherwise could be used to fuel growth the following year. The second possibility could reflect the influence of low temperatures on increasing snowpack at winter's start, which could relate to the aforementioned positive associations between previous November and current January precipitation and growth. Whatever the cause, our findings are in accordance with findings for sugar maple in nearby Canada where negative correlations between growth and previous December temperatures were also noted (Takahashi and Takahashi, 2016).

Whereas it is hard to discern dramatic changes in projected suitable habitat for American chestnut with climate change using the Climate Change Tree Atlas (Prasad et al., 2007-ongoing), other modeling efforts have produced more definitive projections of the distribution of the species as the climate changes. For example, using maximum entropy species distribution modeling, Noah et al. (2021) forecasted the loss of ideal habitat for American chestnut through large areas of the southern and mid portions of the species' range but some gains in the north by 2100. Using species distribution modeling, Barnes and Delborne (2019) similarly projected range contraction within the species' traditional range but an expansion in the north by 2080. Notably, results from this latter projection proposed that American chestnut would be primarily a Canadian species by the end of the century. Although Dalglish et al. (2016) also projected northern expansion of American chestnut, they noted that this is unlikely without human assisted migration due to the limited availability of seed in native habitats.

It is with this background of possible northern expansion of suitable habitat, but the likely need for assisted migration of American chestnut to facilitate this, that the question of seed source selection to support adequate growth and survival in the north arises. Results from our provenance planting suggest that, under current climate conditions, moderate temperature zone sources showed growth potentials equal to fast growing warm temperature zone sources, but with a lower risk of winter shoot injury – a potential beneficial combination. However, as climate conditions change over time, it is unclear that contemporary patterns of source performance will persist. Indeed, provenance trials that are broadly spatially replicated (which serves as a space for climate substitution) often show that source performance is not always

consistent across climate gradients (Wright 1976). Furthermore, source performance may stray even further from historic norms as trees experience unique climate variations and extremes (e.g., high temperature, droughts, freeze-thaw cycles) beyond the current record. These and other levels of known and unknown complexity make source recommendations moving forward fraught with challenge and uncertainty.

## 5. Conclusion

Regardless of genetic source, American chestnut had some inherent vulnerability to both winter shoot freezing injury and spring leaf frost damage. The level of susceptibility varied among genetic sources, with sources from warm temperature zones generally having the greatest risk of damage. Warm temperature zone sources also often experienced budbreak and leaf-out that was earlier in the season and that occurred following fewer GDD. Genetic sources sometimes differed in growth, but differences were modest compared to the high overall growth potential. Growth was generally higher with a lengthened growing season (earlier budbreak and leaf out), but was depressed following elevated shoot winter injury. Although considered a relatively drought tolerant species (Wang et al., 2013), correlations with climate factors highlight the positive influence on adequate moisture availability (primarily for periods prior to ring formation) on American chestnut growth. With only a few exceptions, temperature zone sources generally followed similar patterns of association between moisture availability and growth. In general, trees from the moderate temperature zone tended to have low foliar frost and shoot winter injury while also exhibiting exemplary growth. This combination may allow for improved competitive success – even in cold northerly environments like our planting site.

### *CRedit authorship contribution statement*

**Paul G. Schaberg:** Conceptualization, Methodology, Investigation, Writing – original draft, Supervision, Funding acquisition. **Paula F. Murakami:** Conceptualization, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – review & editing, Visualization, Project administration. **Kendra M. Collins:** Validation, Investigation, Resources, Writing – review & editing. **Christopher F. Hansen:** Investigation, Writing – review & editing. **Gary J. Hawley:** Conceptualization, Methodology, Investigation, Writing – review & editing.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgements

We are grateful to staff from the Green Mountain National Forest for their help with establishing the progeny test used for this study. We also thank Dan Hale, Jill Spies, Jamie Van Cleif, Liana Vitousek and Deni Rangeulova for their assistance with field assessments and Harry Silbaugh for his help collecting tree increment cores. This research was supported by funds provided by the USDA Forest Service Northern Research Station, the USDA CSREES McIntire-Stennis Forest Research Program (grant 1020600), and The American Chestnut Foundation (grants 2012-6 and 2018-3). Tree ring datasets will be available for download from The Dendroecological Network at <https://www.uvm.edu/femc/dendro>.

### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120178>.

## References

- Anagnostakis, S.L., 1987. Chestnut blight: the classical problem of an introduced pathogen. *Mycologia* 79 (1), 23–37.
- Barnes, J.C., Delborne, J.A., 2019. Rethinking restoration targets for American chestnut using species distribution modeling. *Biodiver. Conservat.* 28 (12), 3199–3220.
- Beattie, R.K., Diller, J.D., 1954. Fifty years of chestnut blight in America. *J. For.* 52, 323–329.
- Belair, E.D., Saunders, M.R., Bailey, B.G., 2014. Four-year response of underplanted American chestnut (*Castanea dentata*) and three competitors to midstory removal, root trenching, and weeding treatments in an oak-hickory forest. *For. Ecol. Manage.* 329, 21–29.
- Braun, E.L., 1950. Deciduous forests of Eastern North America. *Soil Science* 71 (2), 155. <https://doi.org/10.1097/00010694-195102000-00012>.
- Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2016. dplR: Dendrochronology Program Library version 1.6.4. <http://CRAN.R-project.org/package=dplR>.
- Buttrick, P.L., 1925. Chestnut in North Carolina, in Chestnut and the chestnut blight in North Carolina, Pap. No. 56. North Carolina Geological and Economic Survey, Raleigh, NC, pp. 6–10.
- Comerford, D.P., Schaberg, P.G., Templer, P.H., Socci, A.M., Campbell, J.L., Wallin, K.F., 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. *Oecologia* 171 (1), 261–269.
- Cook, E.R., Peters, K., 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. <https://repository.arizona.edu/handle/10150/261038> (accessed August 2018).
- Cook, B.I., Smerdon, J.E., Seager, R., Coats, S., 2014. Global warming and 21st century drying. *Climate Dyn.* 43 (9–10), 2607–2627.
- Dalgleish, H.J., Nelson, C.D., Scriver, J.A., Jacobs, D.F., 2016. Consequences of shifts in abundance and distribution of American chestnut for restoration of a foundation forest tree. *Forests* 7 (1), 4. <https://doi.org/10.3390/f7010004>.
- Elliston, J.E., 1981. Hypovirulence and chestnut blight research: fighting disease with disease. *J. For.* 79, 657–660.
- Griffin, G.J., 2000. Blight control and restoration of the American chestnut. *J. For.* 98, 22–27.
- Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: A manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* 57 (2), 205–221.
- Gurney, K.M., Schaberg, P.G., Hawley, G.J., Shane, J.B., 2011. Inadequate cold tolerance as a possible limitation to American chestnut restoration in the northeastern United States. *Restoration Ecol.* 19 (1), 55–63.
- Herms, D.A., Mattson, W.J., 1992. The Dilemma of Plants: To Grow or Defend. *Quarterly Rev. Bio.* 67 (3), 283–335.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.
- Jacobs, D.F., 2007. Toward development of silviculture strategies for forest restoration of American chestnut (*Castanea dentata*) using blight-resistant hybrids. *Biolog. Conserv.* 137, 497–506.
- Jacobs, D.F., Severeid, L.R., 2004. Dominance of interplanted American chestnut (*Castanea dentata*) in southwestern Wisconsin. *USA. For. Ecol. Manage.* 191 (1–3), 111–120.
- Janowiak, M.K., D'Amato, A.W., Swanson, C.W., Iverson, L., Thompson, F.R., Dijk, W. D., Matthews, S., Peters, M.P., Prasad, A., Fraser, J.S., Brandt, L.A., Butler-Leopold, P., Handler, S.D., Shannon, P.D., Burbank, D., Campbell, J., Cogbill, C., Duveneck, M.J., Emery, M.R., Fischelli, N., Foster, J., Hushaw, J., Kenefic, L., Mahaffey, A., Morelli, T.L., Reo, N.J., Schaberg, P.G., Simmons, K.R., Weiskittel, A., Wilmot, S., Hollinger, D., Lane, E., Rustad, L., Templer, P.H., 2018. New England and northern New York forest ecosystem vulnerability assessment and synthesis: a report from the New England Climate Change Response Framework project. USDA Forest Service. Gen. Tech. Rep. NRS-173. Northern Research Station Newtown Square, PA.
- Keever, C., 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains. *Ecology* 34, 44–45.
- Kudo, K., Yasue, K., Hosoo, Y., Funada, R., 2015. Relationship between formation of earlywood vessels and leaf phenology in two ring-porous hardwoods, *Quercus serrata* and *Robinia pseudoacacia*, in early spring. *J. Wood Sci.* 61 (5), 455–464.
- Kuhlman, E.G., 1978. The devastation of American chestnut by blight, in: MacDonald, W. L., Cech, F.C., Luchok, J., Smith, C. (Eds), Proceedings of the American Chestnut Symposium, West Virginia University, Morgantown, WV, pp. 1–3.
- Little, E.L., 1977. Atlas of United States trees, Vol. 4. Minor eastern hardwoods. Maps 27-NE and 27-SE. USDA Misc. Publ. 1342., Washington, DC.
- MacDonald, W.L., Fulbright, D.W., 1991. Biological control of chestnut blight: use and limitations of transmissible hypovirulence. *Plant Dis.* 75, 656–661.
- McEwan, R.W., Keiffer, C.H., McCarthy, B.C., 2006. Dendroecology of American chestnut in a disjunct stand of oak-chestnut forest. *Can. J. For. Res.* 36 (1), 1–11.
- Miller, P., Lanier, W., Brandt, S., 2001. Using Growing Degree Days to Predict Plant Stages. Pamphlet MT200103AG, Communications Services. Montana State University, Bozeman, Bozeman, MT.
- Newhouse, A.E., Polin-McGuigan, L.D., Baier, K.A., Valletta, K.E.R., Rottmann, W.H., Tschaplinski, T.J., Maynard, C.A., Powell, W.A., 2014. Transgenic American chestnuts show enhanced blight resistance and transmit the trait to T1 progeny. *Plant Sci.* 228, 88–97.
- NOAA National Centers for Environmental Information, 2020. Climate at a Glance: County Time Series. <https://www.ncdc.noaa.gov/cag> (accessed 15 April 2020).
- Noah, P.H., Cagle, N.L., Westbrook, J.W., Fitzsimmons, S.F., 2021. Identifying resilient restoration targets: Mapping and forecasting habitat suitability for *Castanea dentata* in Eastern USA under different climate-change scenarios. *Climate Change Ecol.* 2, 100037. <https://doi.org/10.1016/j.ecoehg.2021.100037>.
- Nowosad, J., 2018. Pollen: Analysis of Aerobiological Data. R package version 0.71.0. <https://CRAN.R-project.org/package=pollen>.
- Pederson, N., Bell, A.R., Cook, E.R., Lall, U., Devineni, N., Seager, R., Eggleston, K., Vranes, K.P., 2013. Is an Epic Pluvial Masking the Water Insecurity of the Greater New York City Region? *J. Climate* 26 (4), 1339–1354.
- Prasad, A.M., Iverson, L.R., Matthews, S., 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, OH. <https://www.nrs.fs.fed.us/atlas/tree/>.
- PRISM Climate Group, 2020. PRISM climate data. <http://prism.oregonstate.edu> (accessed 14 February 2020).
- Reinmann, A.B., Susser, J.R., Demaria, E.M.C., Templer, P.H., 2018. Declines in northern forest tree growth following snowpack decline and soil freezing. *Global Change Bio.* 1–11.
- Rice, G., McCoy, A., Webb, T., Bond, C., Speed, V., 1980. Memories of the American chestnut, Foxfire 6th ed., In: Anchor Press/Doubleday Press, Garden City, NY, pp. 397–421.
- Russell, E.W.B., 1987. Pre-blight distribution of *Castanea dentata* (Marsh.) Borkh.) *Bullet. Torrey Botanical Club* 114 (2), 183. <https://doi.org/10.2307/2996129>.
- Saielli, T.M., Schaberg, P.G., Hawley, G.J., Halman, J.M., Gurney, K.M., 2014. Genetics and silvicultural treatments influence the growth and shoot winter injury of American chestnut in Vermont. *For. Sci.* 60 (6), 1068–1076.
- Smith, D.M., 2000. American chestnut: ill-fated monarch of the eastern hardwood forest. *J. For.* 98 (2), 12–15.
- Stern, R.L., 2019. Evaluating climate and environmental drivers of tree species growth in the Northern Forest. University of Vermont, Burlington, VT, USA, p. 189 p. Ph.D. Dissertation.
- Stern, R.L., Schaberg, P.G., Rayback, S.A., Murakami, P.F., Hansen, C.F., Hawley, G.J., 2020. Growth of canopy red oak near its northern range margin: current trends, potential drivers and implications for the future. *Can. J. For. Res.* 50, 975–988.
- Stern, R.L., Schaberg, P.G., Rayback, S.A., Murakami, P.F., Hansen, C.F., Hawley, G.J., 2021. Eastern white pine and eastern hemlock growth: possible tradeoffs in response of canopy trees to climate. *Can. J. For. Res.* 51 (12), 1926–1938.
- Stokes, M., Smiley, T., 1968. An Introduction to Tree-Ring Dating. University of Chicago Press, Chicago, IL.
- Suzuki, M., Yoda, K., Suzuki, H., 1996. Phenological comparison of the onset of vessel formation between ring-porous and diffuse-porous deciduous trees in a Japanese temperate forest. *Iawa J.* 17 (4), 431–444.
- Takahashi, S., Okada, N., Nobuchi, T., 2015. Relationship between vessel porosity and leaf emergence pattern in ring-and diffuse-porous deciduous trees in a temperate hardwood forest. *Botany* 93 (1), 31–39.
- Takahashi, K., Takahashi, H., 2016. Effects of climatic conditions on tree-ring widths of three deciduous broad-leaved tree species at their northern distribution limit in Mont St. Hilaire, eastern Canada. *J. For. Res.* 21 (4), 178–184.
- USDA Agricultural Research Service, 2018. <http://planthardiness.ars.usda.gov/PHZMWeb/> (accessed 29 July 2018).
- Vermont Agency of Natural Resources Department of Forest Parks and Recreation, 2015. Forest insects and disease conditions in Vermont 2015. Waterbury, VT.
- Vicente-Serrano, S.M., Begueria, S., López-Moreno, J.I., 2017. Global SPEI Database. <http://spei.csic.es/database.html> (accessed 17 July 2017).
- Wang, G., Knapp, B.O., Clark, S.L., Mudder, B.T., 2013. The Silvics of *Castanea dentata* (Marsh.) Borkh., American chestnut, Fagaceae (Beech Family). USDA Forest Service Gen. Tech. Rep. SRS-173, Southern Research Station Asheville, NC.
- West, P.W., 1980. Use of diameter increment and basal area increment in tree growth studies. *Can. J. For. Res.* 71–77.
- West, N.E., Wein, R.W., 1971. A plant phenological index technique. *BioScience* 21 (3), 116–117.
- Westbrook, J.W., Holliday, J.A., Newhouse, A.E., Powell, W.A., 2020. A plan to diversify a transgenic blight-tolerant American chestnut population using citizen science. *Plants People Planet* 2 (1), 84–95.
- Westbrook, J.W., James, J.B., Sisco, P.H., Frampton, J., Lucas, S., Jeffers, S.N., 2019. Resistance to *Phytophthora cinnamomi* in American chestnut (*Castanea dentata*) backcross populations that descended from two Chinese chestnut (*Castanea mollissima*) sources of resistance. *Plant Dis.* 103 (7), 1631–1641.
- Wright, J.W., 1976. Introduction to Forest Genetics. In: Introduction to Forest Genetics. Elsevier, pp. 1–6. <https://doi.org/10.1016/B978-0-12-765250-4.50005-8>.
- Yamaguchi, D.K., 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* 21 (3), 414–416.
- Zang, C., Biondi, F., 2015. Treeclim: an R package for the numerical calibration of proxy-climate relationships. *Ecography* 38 (4), 431–436.
- Zimmerman, M.H., 1983. Xylem structure and the ascent of sap. Springer-Verlag, New York.