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Assessing the influence of climate on the growth of green ash trees from five Plant Hardiness Zones growing in a range-wide provenance test near the species' northern range limit

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Abstract

Green ash is threatened with extirpation from emerald ash borer (EAB) attack. Because green ash has an extensive range, its restoration could require both breeding for EAB resistance and possible adaptation to a variety of environmental gradients. We assessed the growth and climate sensitivity of green ash from five Plant Hardiness Zones (PHZs) growing in a range-wide provenance test in Vermont. Although there tended to be greater growth among trees from the warmest PHZ (7), differences were rarely statistically distinguishable. For trees from all PHZs, growth was positively correlated with precipitation in the current year and negatively correlated with precipitation the year before (a possible legacy effect). Growth was negatively associated with temperature the year of ring formation but positively associated with temperatures the year before. Growth was often positively correlated with winter snow but was negatively associated with spring or fall snow for the warmest PHZs. Climate correlations for PHZ 3 were unusual in that (1) only positive correlations were detected, (2) no legacy effects were noted, and (3) despite being from the coldest region, no correlations with snow were found. Growth increased over time for the warmest PHZs during a period of simultaneous increases in temperature and precipitation.

Key words: *Fraxinus pennsylvanica*, tree rings, precipitation, temperature, snow

Introduction

Green ash (*Fraxinus pennsylvanica* Marsh.) has an extensive range—from southern Alberta, Canada east to Nova Scotia and south to Florida and across to Texas (Burns and Honkala 1990). Although typically considered a moist bottomland or stream bank tree, green ash can be found on a wide variety of soil and site conditions across its vast range (Burns and Honkala 1990). Green ash wood is strong, hard, and shock resistant, and has excellent bending qualities, so it has had many uses (Burns and Honkala 1990). Green ash is one of the most widely planted hardwoods for windbreaks, and it has been widely planted in urban and suburban landscapes as a replacement tree for American elm (*Ulmus americana* L.) following its widespread loss to Dutch elm disease (Poland and McCullough 2006). The species also has great importance to wildlife because its seeds provide food for a number of game and nongame species (Burns and Honkala 1990). However, the many benefits that green ash provide are now threatened due to the high likelihood of mortality following infestation by the emerald ash borer (EAB; *Agrilus planipennis*).

The EAB is a green buprestid beetle native to Northeastern Asia that was introduced to North America sometime before 2002 (Cappaert et al. 2005). In its larval form, EAB feeds on the cambium, phloem, and xylem of ash (*Fraxinus* spp.) trees before exiting the bark as adults (Cappaert et al. 2005). Larval galleries gradually encircle the boles of trees, typically leading to girdling and tree death. Although all North American ash are highly susceptible to EAB-induced damage and mortality, green ash appears to be particularly vulnerable (Anulewicz et al. 2007). To safeguard the many direct and indirect benefits that green ash bring to rural and urban landscapes, a comprehensive restoration program is needed. For example, Romero-Severson and Koch (2017) have suggested a three-stage process: (1) visual identification and experimental verification of resistance in lingering ash, (2) the combination of resistance alleles through controlled pollination, and (3) the planting of the most resistant tree lines in "polycross" orchards to produce seed that can be exported for field trials. The goal is the development of genetically diverse EAB-resistant lines that are also locally adapted to the multitude of site conditions across the species' range (Romero-Severson and Koch 2017). For example, green ash once grew from USDA Plant Hardiness Zone (PHZ) 9b, with a 30-year average annual minimum temperature as high as −1.1 °C, to zone 3a with a 30-year average annual minimum temperature as low as −40 °C (United States Department of Agriculture (USDA), Agricultural Research Service 2018). Considering this almost 39 °C range in minimum temperature exposure and adaptation, it seems likely that matching hardiness levels of restoration stock to the hardiness zone of a planting site would be important to prevent freezing injury that could limit tree growth and vigor.

One way of assessing broad patterns of adaption, including relative climate sensitivity, is to measure tree performance in range-wide provenance tests (Wright 1976), where genetic sources from across a species' range are planted together in a common garden. Because environmental conditions are relatively homogeneous in such a planting, differences in tree performance associated with genetics can be more clearly isolated. Multiple green ash provenance tests have been established over the years, and preliminary results from these have highlighted several tendencies in performance among genetic sources. For example, Wright (1944) noted that green ash from the northern ecotype experienced slow growth, a high resistance to winter mortality and early autumnal leaf fall relative to trees from the southern coastal plain ecotype. Similarly, Geyer et al. (2005) found that trees from southern sources were generally larger but were more prone to winter shoot injury. They also reported that growth was best when sources were planted up to three degrees of latitude north of the seed source's origin—a distance where the likelihood of winter injury did not increase. In contrast, Steiner et al. (1988) found that green ash from southern Ontario and the "central plains" (eastern Nebraska to central Illinois) were the tallest after 6 years of growth relative to sources from the northeastern and southern regions. They also noted that trees originating south of planting sites did not exhibit a consistent growth advantage. Results from Steiner et al. (1988) are particularly pertinent because it was a very large experiment (48 seed sources) planted across 10 common garden locations that included the Vermont provenance test examined here.

In addition to genetics, tree performance can be greatly influenced by yearly variations in climate, and tree-ring data can provide a high-resolution retrospective view of climate-growth relationships for tree communities (e.g., Stern et al. 2020, 2021). Recently, tree ring and climate data were used to test for the comparative climate sensitivities in a range-wide provenance test of another tree species put at risk by an exotic stressor—American chestnut (*Castanea dentata* (Marsh.) Borkh.) threatened by chestnut blight caused by the fungal pathogen *Cryphonectria parasitica* (Murr.) Barr. Here, growth was compared for seed sources from native stands that originated from warm, moderate, and cold winter temperature zones (Schaberg et al. 2022). There was a consistent trend for trees from the cold temperature zone to grow less than trees from the other temperature zones. Even though American chestnut is a relatively drought-tolerant species, growth of trees from all temperature zones was positively correlated with precipitation inputs the year before and occasionally the year of ring formation (Schaberg et al. 2022). In contrast, growth appeared to be less affected by temperature.

A better understanding of the relative influences of genetics and climate on green ash growth is particularly important to document now because EAB infestation is greatly diminishing green ash populations (Anulewicz et al. 2007), including in range-wide provenance tests (Steiner et al. 2019). Indeed, as green ash provenance tests are removed from the landscape, the knowledge gained from those remaining is becoming more novel and important. Here we describe the use of xylem increment cores to evaluate the influence of PHZ and climate on the growth of green ash in a range-wide provenance trial with no EAB damage that is planted near the north of the species' range in northern Vermont. We hypothesized the following:

H^1—consistent with findings in other provenance tests, that trees from the warmer PHZ sources would have greater growth than trees from colder PHZ sources.

H^2—because sources are likely adapted to climate cues typical of their locations of origin, we propose that the growth of trees from warmer PHZs may respond to temperature, precipitation, and snow conditions differently than trees from colder PHZs. For example, trees from warmer PHZs may show a greater sensitivity to low temperature or snow exposures.

Methods

Site description

The green ash provenance planting was established in 1978 on the campus of the University of Vermont (44°28′27.17″, −73°11′29.11″W; Fig. 1) as a randomized complete block design (4 blocks containing 27 provenances in 4-tree linear plots) using 1:1 stock grown in a Pennsylvania nursery (Steiner et al. 1988). Seed sources were from locations throughout the historical range of green ash. However, due to significant tree mortality from various causes including damage from a severe ice storm in 1998, only nine provenances were included in the current study (Fig. 1). These nine seed sources represented five PHZs—from 3 (the coldest) through 7 (the warmest) (Table 1).

Dendrochronology

In 2019, two xylem increment cores per tree were collected at breast height (1.3 m above the soil surface) from 44 codominant trees representing the 5 PHZs. The specific number of trees sampled per seed source and PHZ are listed in Table 1. Cores were oven-dried, mounted on wooden blocks, and sanded with progressively finer grit sandpaper. 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). The program COFECHA (v6.06p) was used to statistically detect and subsequently correct crossdating errors, as well as calculate chronology statistics (Table 2) (Bunn et al. 2016). Whole ring width (WRW) measurements were averaged per tree and used to calculate basal area increment (BAI (cm^2/year); function bai.out, R package *dplR*;

Fig. 1. Source codes, locations, and plant hardiness zones for the five green ash sources at the Green Mountain National Forest planting. Figure was created using ArcGIS 10.5.1. The spatial distribution of sources is depicted on the map and source codes are from Steiner et al. (1988). More detailed information about sources appears in Table 1. Green ash's native range layer is from Little and Viereck (1971).

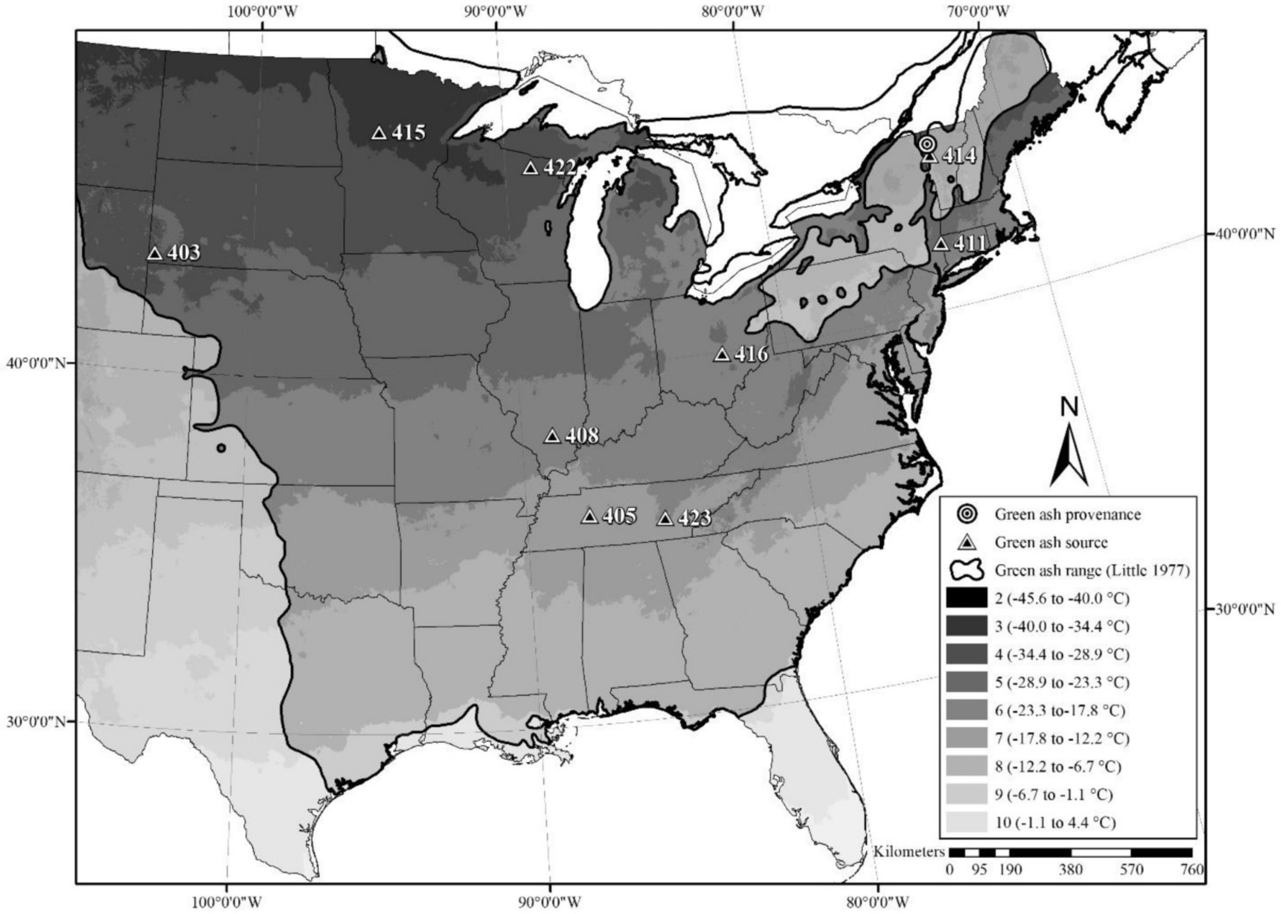


Table 1. Plant Hardiness Zones (PHZs), locations, source codes, and numbers of trees sampled from the green ash provenance test in Burlington, VT.

PHZ	Location	Latitude	Longitude	Source code	*n* trees/source	*n* trees/PHZ
3	Park Rapids, MN	46°55′19.9″N	95°03′31.0″W	415	9	9
4	Edgemont, SD	43°18′04.0″N	103°49′31.8″W	403	4	8
4	Hiles, WI	45°44′53.5″N	88°58′04.1″W	422	4	
5	Amenia, NY	41°50′57.5″N	73°33′24.5″W	411	5	13
5	Charlotte, VT	44°19′11.3″N	73°11′19.3″W	414	8	
6	Bonnie, IL	38°12′10.1″N	88°54′12.2″W	408	5	12
6	Jacksontown, OH	39°57′34.2″N	82°24′46.4″W	416	7	
7	Buffalo, TN	35°53′08.2″N	87°48′24.1″W	405	1	2
7	Pikeville, TN	35°36′20.2″N	85°11′19.7″W	423	1	

Bunn et al. 2016), thereby adjusting for size-related growth trends (West 1980).

For comparisons of growth with temperature and moisture data, WRWs 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.

Table 2. Dendrochronology statistics and crossdating results obtained from COFECHA output.

Dendrochronology statistics
n PHZs = 5
n trees = 44
n cores = 82
Chronology span = 1980–2019
Interseries correlation = 0.444
Mean sensitivity = 0.235
First-order auto-correlation = 0.791

Note: Although 88 cores were collected, some cores were excluded from later analyses because they did not crossdate well with the overall dataset. PHZs, Plant Hardiness Zones.

Statistical analyses

Analyses of variance (ANOVAs) were conducted to ascertain differences in BAI growth among PHZs using JMP Pro 15 statistical software (SAS Institute, Inc., Cary, NC). The assumptions of ANOVAs were tested and nonparametric comparisons were applied using Steel–Dwass tests for all years in the common timeframe (1985–2019) when variances were unequal. Trends in growth over time were tested using linear regressions. Associations were considered significantly different when $P \leq 0.05$.

Using stationary correlations (function dcc, R package, *treeclim*; Zhang and Bondi 2015), growth for each PHZ was associated with temperature and precipitation data (from 1985 to 2019) (PRISM Climate Group 2020). Monthly maximum temperature (Tmax; °C), mean temperature (Tmean; °C), minimum temperature (Tmin; °C), and precipitation (mm) beginning in April the year prior to increment core collection and ending in September of the year of annual ring formation were correlated with growth for each PHZ. Additionally, we correlated growth with snow duration (number of days when snow depth was greater than 2.54 cm) and monthly total snowfall (cm) for the same timeframe using data obtained from NOAA Online Weather Data (Applied Climate Information System 2021). Trends in climate parameters over time were tested using linear regressions. Associations were considered significantly different when $P \leq 0.05$.

Results

Although visually it appeared at times that trees in PHZs 6 and 7 had higher BAI growth than trees in other sources, there were few significant differences in growth among sources from the different PHZ zones (Fig. 2). Indeed, significant differences were only detected in 1996 when growth of trees from PHZ 5 were greater than for trees in PHZ 3 ($P = 0.0489$) and PHZ 4 ($P = 0.0391$). This general lack of significant differences was attributable to the high variation in growth among trees within PHZ sources, especially PHZ 7 (Fig. 2). PHZ 7 also exhibited higher variation in growth among seed sources within it (e.g., standard errors (SEs) sometimes four times that of other PHZs by the end of the chronology). Although not statistically different, during the 2010s (a period of high growth overall), average BAI levels for trees in the warmest PHZ (7) were almost two times higher than those for trees in the coldest zone (3). Maximum average growth within the plantation overall was 18.2 cm^2 in 2008, whereas maximum growth for PHZ 3 trees was 22.9 cm^2 in 1984 and was 42.2 cm^2 for PHZ 7 trees in 2011. While BAI growth in individual years was rarely different among the PHZs, trends in growth over time did show some divergent patterns among trees from the five PHZs (Fig. 3). Although regression slopes were significantly different from zero for all the PHZs, they were negative or near neutral for the coldest PHZs (slope = −0.1703 for PHZ 3, = 0.0917 for PHZ 4, and = −0.1019 for PHZ 5). In contrast, slopes of growth over time were positive and steeper for the warmer PHZs (slope = 0.2001 for PHZ 6 and = 0.8841 for PHZ 7).

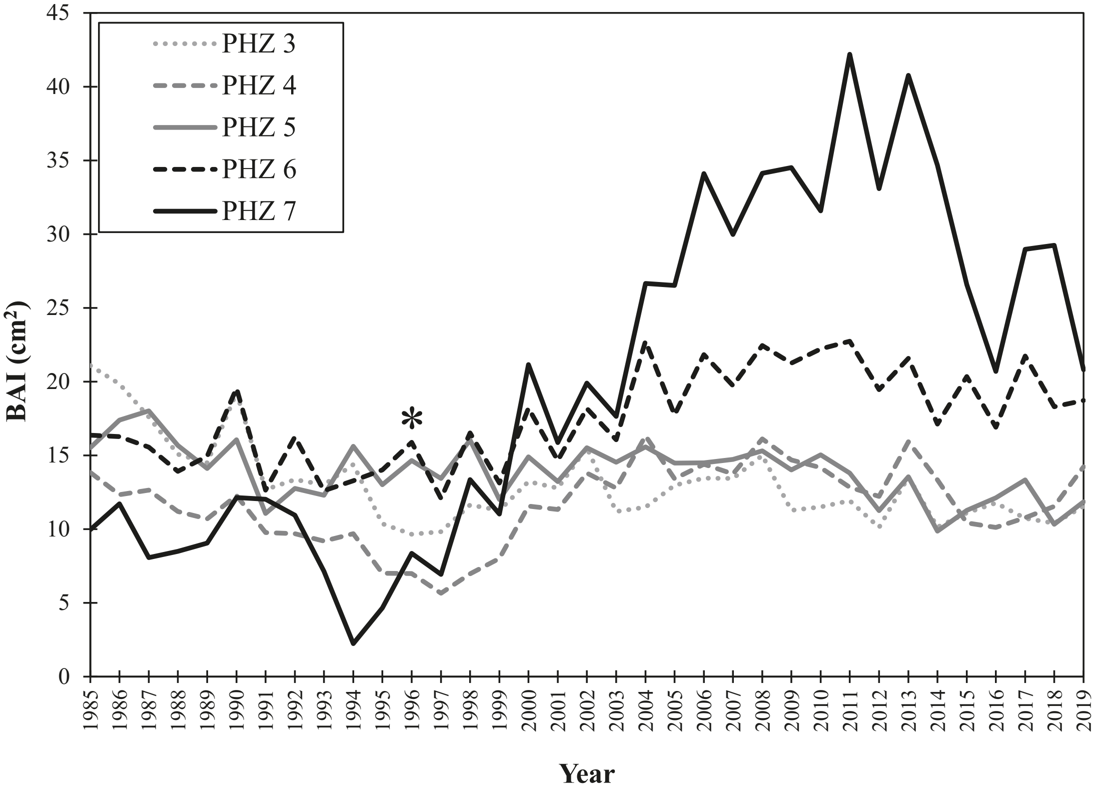
Despite few statistically significant differences in the magnitude of growth, correlation analyses of growth with precipitation, temperature, and snow data did reveal some differences in response among PHZ sources to climate cues. Relative to precipitation, the coldest PHZ 3 source had only positive associations between current year precipitation and growth (Table 3). In contrast, for PHZs 4 and higher, there were generally a mix of negative associations of growth with previous year precipitation and positive associations with current year precipitation. Regarding temperature, the coldest PHZ 3 source had only positive associations of growth with previous year spring and fall temperatures (Table 3). However, for sources from PHZ 4 and higher, there were generally a mix of positive associations of growth with previous year's temperatures (typically in summer), and negative associations of growth with current year temperature (almost exclusively in summer). For snow, there were no significant associations between snow and growth for the coldest two PHZs (3 and 4), whereas there were a mix of positive (with winter snow measures) and negative (for fall and spring snow measures) for sources from PHZs 5 and higher (Table 3). Regression analyses revealed significant positive increases over time for all climate parameters except snowfall (Fig. 4). Slopes of regression lines were modest for the three temperature parameters (0.0360 for Tmax, 0.0480 for Tmean, and 0.0576 for Tmin), whereas the slope of precipitation over time was far steeper (0.6913).

Discussion

BAI growth

Growth was low when seedlings were first planted but increased and then generally plateaued thereafter (Fig. 2). Maximum growth within the plantation overall was in 2008 when the average BAI increment was 18.2 cm^2. As expected, this growth was comparable to maximum levels reported for many northern hardwood species within Vermont (e.g., *Acer saccharum* Marsh. (17.7 cm^2), *Acer rubrum* L. (18.5 cm^2), *Betula alleghaniensis* Britton (17.3 cm^2), and *Fagus grandifolia* Ehrh. (16.2 cm^2) (Stern et al. 2023)). However, green ash growth in this study was less than other species such as *Quercus rubra* L. (26.2 cm^2; Stern et al. 2020) and *Castanea dentata* (Marsh.) Borkh. (34 cm^2; Schaberg et al. 2022) that are noted for their high productivity. Maximum growth for PHZ 7 trees was

Fig. 2. Mean basal area increment (BAI) (cm^2) of green ash growing in a provenance planting on the campus of the University of Vermont, Burlington, VT. Individual lines represent BAI for respective seed source Plant Hardiness Zones (PHZs). ∗The only year when growth among the PHZs was significantly different was 1996 when growth of trees in PHZ 5 was significantly greater than that for trees in PHZ 4 and 3.

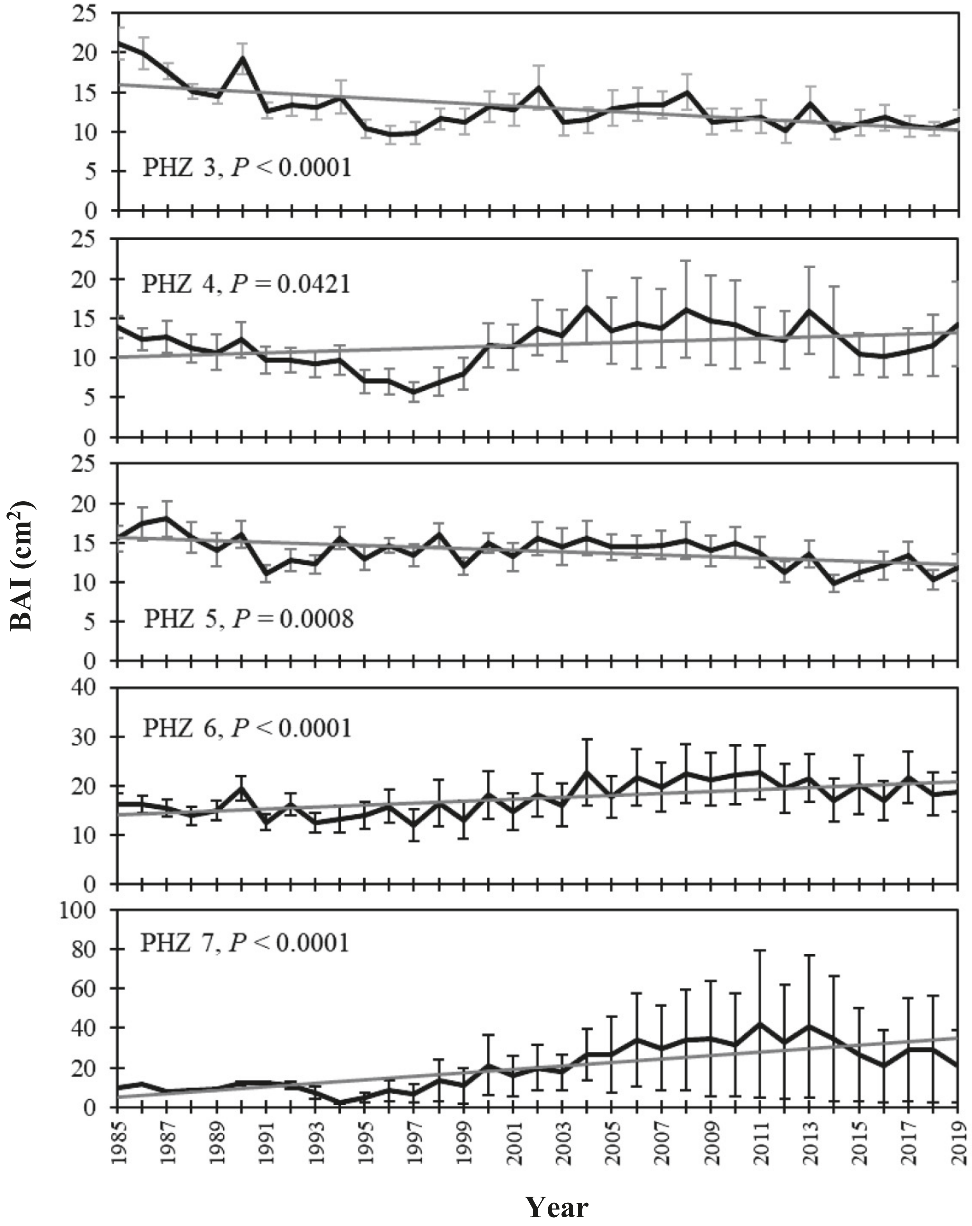


42.2 cm^2 in 2011—an unexpectedly high level that rivaled fast growing *Pinus strobus* L. in Vermont (40.7 cm^2 in 2012) (Stern et al. 2021). The maximum growth rates reported for species other than green ash were for trees of differing ages, at different sites, and for a variety of years. They are reported here for general comparative purposes.

We had hypothesized that trees from warmer PHZ sources would exhibit growth that exceeded trees from colder PHZs because of a general tradeoff between growth and protection that has been documented for many tree species (Wright 1976). Although maximum growth for trees from PHZ 7 was approximately double the maximum growth for trees from PHZ 3, high variation in growth among trees within PHZs made it impossible to consistently detect significant differences in growth based on PHZ (H^1). Variation in growth was especially high among trees from PHZ 7— chiefly during the second half of the chronology. PHZ 7 included only two trees (four cores), so high variation around the mean was not unexpected. Few trees from PHZ 7 were available for sampling because of the high mortality within the plantation for this warmest PHZ seed source. Despite being planted near the north of the species' range limit, winter shoot injury was not monitored for this planting, which was started and monitored by another research group. However, severe winter injury has been noted elsewhere for green ash that originated two degrees (Steiner et al. 1988) or more (Geyer et al. 2005) south in latitude from the planting site. Indeed, winter injury has been associated with increased tree mortality at far northerly sites (Geyer et al. 2005) and among populations from the distant south (Wright 1944)—circumstances similar to the PHZ 7 trees in our study.

It has been proposed that plants can encounter an ecological tradeoff between allocating resources (e.g., nutrients) and energy (e.g., nonstructural carbohydrates) toward growth versus the formation of protective compounds (Herms and Mattson 1992). In particular, this tradeoff has been examined regarding the generalized responses of tree species to temperatures that influence latitudinal range limits (Loehle 1998), as well as differences in cold tolerance among populations within species (Howe et al. 2003). Evidence of this tradeoff relative to growth and cold tolerance has been documented through provenance studies for a broad range of tree species (e.g., Wright 1976; Schaberg et al. 2022), including earlier studies with green ash (Wright 1944; Geyer et al. 2005). Furthermore, these generally report that seed sources from southern regions show greater growth but are more vulnerable to cold injury than seed sources from the north (Wright 1944; Wright 1976; Geyer et al. 2005), though this has not been uniformly observed (e.g., Steiner et al. 1988).

Fig. 3. Mean basal area increment (BAI) (cm^2; solid black lines) of green ash by Plant Hardiness Zone (PHZ) growing in a provenance planting on the campus of the University of Vermont, Burlington, VT. Error bars indicate ±1 SE. Solid grey lines and *P* values represent regression analyses for respective PHZs. Regression lines of growth over time (and associated *P* values of whether regression slopes were significantly different from 0) are also displayed. Note that the *y*-axis scales are different for PHZs 6 and 7.



Climate correlations

Precipitation

Although green ash is native to areas receiving a wide range of precipitation levels (e.g., 380 to 1520 mm per year), it is generally considered a bottomland species that occurs most commonly on alluvial soils along rivers and streams (Burns and Honkala 1990). Considering this, it was not surprising that the growth of green ash from all PHZs was positively correlated with precipitation during the year of ring formation. For green ash from PHZs other than 3, there were also negative correlations of precipitation for some summer months in the year before ring formation with growth the following year. Positive correlations of precipitation and growth the same year highlight the beneficial influence of adequate moisture on woody growth. However, high growth in the current year can leave fewer nonstructural carbohydrates stored within trees to support growth the next year—a possible "legacy effect" that is not uncommon to detect using tree rings (e.g., Kosiba et al. 2018; Stern et al. 2021). More broadly, our findings are in line with larger-scale studies showing the great importance of growing season moisture on broadleaf tree growth in the northeastern US (Martin-Benito and

Table 3. Significant stationary correlations of radial growth with monthly precipitation, snow duration, snowfall, Tmax, Tmean, and Tmin ($P \leq 0.05$) from 1985 to 2019.

		Climate parameter					
PHZ	Month	Precip	Snow duration	Snowfall	Tmax	Tmean	Tmin
3 ($n = 9$)	may	–	–	–	–	0.338	–
	sep	–	–	–	0.366	0.312	–
	FEB	0.479	–	–	–	–	–
	JUN	0.396	–	–	–	–	–
	JUL	0.256	–	–	–	–	–
4 ($n = 8$)	jul	– 0.264	–	–	–	–	–
	aug	– 0.320	–	–	0.373	0.356	–
	sep	–	–	–	0.324	0.294	–
	MAY	0.497	–	–	–	–	–
	JUN	–	–	–	– 0.381	– 0.372	– 0.274
5 ($n = 13$)	apr	–	–	–	–	– 0.287	– 0.398
	jun	– 0.304	–	–	–	–	–
	JAN	–	–	0.432	–	–	–
	FEB	0.339	–	–	–	–	–
	MAY	–	–	–	– 0.309	–	– 0.278
	JUN	0.381	–	–	– 0.340	–	–
	JUL	0.359	–	–	– 0.296	–	–
6 ($n = 12$)	jun	– 0.349	–	–	0.252	–	–
	jul	–	–	–	0.288	–	–
	aug	–	–	–	0.276	0.284	0.295
	nov	–	– 0.347	– 0.356	–	–	–
	dec	–	0.443	0.482	– 0.408	– 0.387	–
	MAR	–	– 0.366	–	–	–	–
	MAY	0.487	–	–	–	–	–
	JUN	–	–	–	– 0.467	– 0.377	–
	JUL	0.323	–	–	– 0.266	–	–
7 ($n = 2$)	jun	–	–	–	0.425	–	–
	jul	– 0.370	–	–	0.389	0.321	–
	oct	0.399	–	–	–	–	–
	MAR	–	– 0.446	–	–	–	–
	APR	0.288	–	–	–	–	0.302
	MAY	0.464	–	–	–	–	–
	JUN	–	–	–	– 0.439	– 0.462	– 0.354

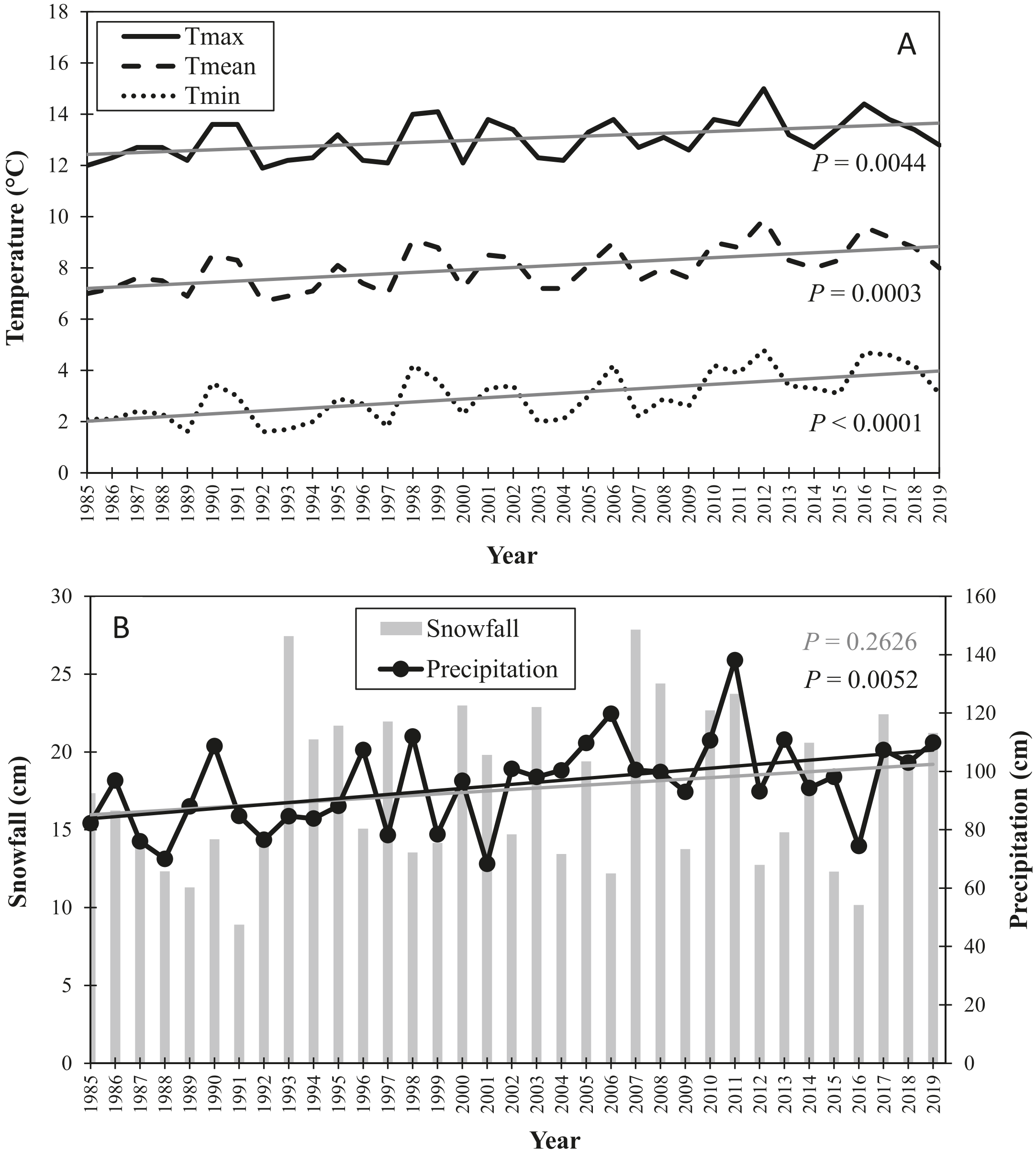
Note: Previous year correlations are indicated by lowercase letters while current year correlations are represented by uppercase letters. Correlation coefficients (*r*) are only listed for months where a significant relationship occurred. Dashes indicate no significant correlation. Number of trees per PHZ is indicated by *n*. PHZ, Plant Hardiness Zone.

Pederson 2015; D'Orangeville et al. 2018) and Europe (e.g., Mette et al. 2013). Although precipitation is projected to increase in coming decades as the climate changes, it is projected to occur with greater intensity and periodicity (Janowiak et al. 2018)—a combination that could decrease water infiltration into soils and create dry periods between intense rains that constrain tree growth despite overall wetter conditions.

Temperature

As with precipitation, there was a tendency for the directionality of correlations with temperature to differ between current and previous year data, but here growth associations tended to be positive with previous year's temperatures (except for PHZ 5), and negative with current year temperatures. In general, negative associations between growth and temperature were more numerous and were related to current year summer data (except for PHZ 6, when Dec Tmax and Tmean were also negatively associated with growth). Negative correlations of growth with current year summer temperatures suggest a sensitivity to heat stress—something that has been documented with other tree species in the northeast (e.g., Stern et al. 2020; Stern et al. 2021). Negative associations of growth with temperature often reflect the influence of heat-induced moisture limitations (Rennenberg et al. 2006), although the presence of these associations during the current pluvial in the northeastern US (Pederson et al. 2013)

Fig. 4. Average annual maximum temperature (Tmax; °C), mean temperature (Tmean; °C), and minimum temperature (Tmin; °C) (A) and average annual snowfall (cm) and precipitation (cm) (B) for Burlington, VT from 1985 to 2019 (PRISM Climate Group 2020; Applied Climate Information System 2021). Regression lines of climate factors over time (and associated *P* values of whether regression slopes were significantly different from 0) are also displayed.



may suggest that direct heat stress is also a factor. Whereas photosynthetic levels increase, then plateau and thereafter decline as temperatures rise, levels of respiration continually rise with temperature (Teskey et al. 2015). When respiration levels outpace photosynthetic gains, associated carbon losses can deplete nonstructural carbohydrate pools that otherwise could fuel growth (Teskey et al. 2015). Temperature constraints on growth could become more prevalent and severe if ambient temperatures rise as projected to occur with climate change (Janowiak et al. 2018).

It is notable that for trees in PHZ 6 there were also negative correlations of growth with temperatures outside of the summer months—December Tmax and Tmean. Although this could be the result of lower temperatures in December resulting in higher growth the following year, it is more likely that this reflects a circumstance where higher December temperatures result in lower growth because higher early winter temperatures delay the development of snowpacks that protect the soil from freezing (see section on snow).

Positive correlations of growth with previous year's temperatures may also represent a "legacy effect" where high temperatures in one year result in low growth that season, but that low growth results in the accumulation of residual nonstructural carbohydrates that can then be used to enhance growth the following year.

Snow

Winter snow was positively correlated with growth for PHZ 5 (current year's January snowfall) and PHZ 6 (previous year's December snow duration and snowfall). In contrast, shoulder season snow was associated with lower growth for PHZ 6 (previous year's November snow duration and snowfall and current year's March snow duration) and PHZ 7 (current year's March snow duration). Research over diverse regions and with a variety of species has shown that snow can insulate the soil from low air temperatures that would otherwise cause soil freezing and root damage that can then reduce aboveground woody growth (e.g., Hennon et al. 2012; Comerford et al. 2013; Stern et al. 2023). Positive correlations for December and January snow data and growth are consistent with this connection, but here is associated with a new species for which this phenomenon, to our knowledge, has not yet been reported. A melting winter snowpack may also provide valuable moisture to help support woody growth at the start of the growing season. It is curious that a positive association between winter snow and growth was not detected for trees from the coldest PHZs assessed—3 and 4. This outcome was unexpected and deserves further assessment to evaluate the possible cause(s) for this differential response. One hypothesis that could be tested is that green ash from PHZs 3 and 4 have had more consistent exposures to low temperatures, so their roots develop greater cold hardiness and are less reliant on snowpacks for protection from cold damage that can then reduce aboveground growth. Other work has shown that different species growing together can differ greatly in their root cold tolerance, and that these differences can modulate their relative vulnerabilities to root freezing injury (Schaberg et al. 2011). These same patterns could well exist among different populations within a species.

Negative correlations of fall and spring snow data with growth for PHZs 6 and 7 are consistent with the possibility that snow can functionally shorten growing seasons—limiting photosynthesis in the fall and delaying budbreak and the start of the growing season in the spring. This association has also been observed with other hardwood species (e.g., Stern et al. 2023). It is interesting that the negative associations with shoulder season (especially current year's March) snow seem specific to the warmest PHZ sources. Summaries of provenance test data for a range of tree species has shown that southern seed sources break bud and leaf out earlier in the year (Wright 1976), so they would be more likely to be negatively impacted by lingering snow. It is projected that climate change will result in less precipitation falling as snow (Janowiak et al. 2018)—a possibility that would reduce the protection of roots during winter but could increase the functional lengths of growing seasons.

Trends over time and possible implications for management

The slopes of linear regressions of growth over time were slightly negative or near neutral for PHZs 3 through 5 but were positive and steeper for PHZs 6 and 7. Regression slopes of four of the five climate factors assessed were significant and positive, with those for the temperature measures being far lower (0.0360 for Tmax, 0.0480 for Tmean, and 0.0576 for Tmin) than that for precipitation (0.6913). It is unclear whether near level or slightly declining growth for trees in the colder PHZs is associated with the changes in temperature and precipitation over time. However, if the two are related, then it could signify that growth for green ash from these colder sources could be somewhat compromised as climate continues to change. In contrast, growth of trees from the warmer PHZs has increased over time synchronous with regional warming and increases in precipitation.

Synthesized results from an array of provenance tests assessed under relatively static climate conditions have shown that sources originating hundreds of miles south of the test plantation often grow faster than more localized sources (Wright 1976). It seems reasonable to predict that this distance of optimal seed source performance could be extended even further as climates warm, though this hypothesis awaits specific testing. We propose that recent increases in growth for green ash from PHZs 6 and 7 may relate to increases in temperature that can extend the growing season and reduce the likelihood of freezing injury. Furthermore, seed sources that are adapted to warmer climates would presumably be less likely to experience heat-related stress (direct temperature stress or heat-induced water stress), especially under conditions of increasing precipitation (Fig. 4). Although trees from PHZs 6 and 7 have historically shown a sensitivity to reduced growth with warmer summer temperatures (Table 3), growth trends over time suggest that this has not necessarily been an undue constraint on recent growth. When breeding for increased EAB resistance and climate adaptation, managers may want to consider how changing climates may interact with historic patterns of temperature and moisture adaptations among regional seed sources. Is it possible that past results of climate-growth relationships are more conservative than the conditions that breeding programs are preparing for? If yes, then inclusions of seed sources from a diverse array of locations, including from PHZs that are warmer than those of the test planting, may help improve the growth of resulting stock, especially as climate change continues.

Conclusions

Better understanding of differences and/or similarities in response of green ash seed sources to climate could help in the restoration of the species following population declines associated with EAB infestation. In general, correlations of growth with climate parameters were relatively consistent across the five PHZs. Factors that were most associated with variations in growth were positive associations with current summer precipitation, negative associations with current summer temperature, and mixed associations with snow—some positive, some negative depending on the season and PHZ. Although the PHZs did have many similar correlation results, trees in PHZ 3 (and sometimes 4) also showed some unique patterns that may relate to differential sensitivities to climate for trees from the coldest zones. For example, trees from PHZ 3 showed only positive associations with growth, suggesting that recent precipitation and temperature levels did not significantly limit growth. Furthermore, there were no legacy effects apparent across years for this source. Finally, trees from PHZ 3 and 4 had no significant correlations with snow data, even though trees originated from regions where winter snowpacks are most pronounced and long-lasting. Another notable trend was an increase in growth over time for trees from the warmest PHZs 6 and 7. This increase coincided with significant increases in temperature and precipitation for the time period, though we have no evidence that these two phenomena are causally related.

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Data availability

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

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Competing interests

The authors declare there are no competing interests.

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