Quercus rubra Seedling Biomass Response Related to Mean Annual Temperature Conditions of Associated Provenance

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Abstract.—*Quercus rubra L.* is a hardwood species found throughout the eastern United States. Although climate change is projected to increase this species' suitable habitat range, current population structures and migration patterns may not be suitable to sustain future forest health. To investigate how populations respond when planted outside of their traditional ranges, we collected seeds from 22 *Q. rubra* populations spanning the species range and planted them in two common garden sites. Ford forest (cooler and drier) and Kellogg Forest (warmer and wetter) sites are located in Michigan's upper and lower peninsulas, respectively. During the 2019 and 2020 growing seasons, *Q. rubra* biomass increased with increasing seed source mean annual temperature (MAT), with a steeper slope at Ford in 2020. We also observed more frost damage at the Ford site in plants that evolved with a higher MAT.

INTRODUCTION

Quercus rubra L. (common name: northern red oak) is a hardwood tree commonly found within forested ecosystems of eastern North America (Little 1971). Climate change not only increases annual temperature averages, it also restructures ecosystems norms (Frelich and Reich 2010, Seddon 2010). For many forest species, suitable habitat is expected to decline because of climate change. However, within eastern North America, an opposite trend is generally projected for many oak species including *Q. rubra*. According to suitable habitat modeling, such as DISTRIB-II and the Parallel Climate modeling, the range of *Q. rubra* is expected to increase by 51 percent and 50 percent under high (4.8 °C increase by 2100) and low (2.6 °C increase by 2100) climate change scenarios, respectively (Collins et al. 2013, Iverson et al. 2008, Peters et al. 2019).

Projected increases in suitable habitat for *Q. rubra* should not be mistaken for climate change readiness. Since the species range is quite expansive, current *Q. rubra* provenances have many distinctive localized adaptations suited for the present/past climate conditions. And although intraspecific gene flow between oak populations may well be maintained through wind pollination, loss of stand density and forest fragmentation pose threats to oaks, including for *Q. rubra* (Fernández and Sork 2007, Gerwein and Kesseli 2006, Oyama et al. 2017). Without human intervention, population health within northern *Q. rubra* provenances may depreciate, posing a real threat to future forests.

Forestry assisted migration is a tool used to prevent species loss or forest fragmentation and increase a species' climate-change adaptive potential. This assisted migration practice includes the movement of populations within current species ranges and into populations located in the leading-edge habitat, i.e., range expansion (Pedlar et al. 2012, Ste-Marie et al. 2011). Because of forestry assisted-migration's specific aims, the risk for introduction of invasive species, diseases, or

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Table 1.—Site locations and seed source mean annual temperature (MAT) specific to *Q. rubra* provenances planted at the Ford and Kellogg common gardens. Provenances are listed based on seed source MAT, highest to lowest. GPS coordinates are listed as latitude, longitude.

Population Name, State	Population ID	GPS	Families (#)	Seed source MAT (°C)
Eagle Mine, MI	13	46.749, -87.891	6	4.1
Dow forest, MI	1	47.425, -88.056	4	4.2
Cliff Drive, MI	3	47.354, -88.350	4	4.3
Baraga Plains, MI	11	46.673, -88.529	3	4.4
Copper Harbor Sand dunes, MI	2	47.440, -88.219	6	4.5
Russell, WI	23	46.768, -91.105	3	4.6
Maasto Hiihto (1), MI	4	47.138, -88.610	6	4.9
Nara Trails (1), MI	5	47.103, -88.520	2	4.9
Nara Trails (2), MI	6	47.107, -88.551	6	4.9
Nara Trails (3), MI	7	47.105, -88.529	5	4.9
Nara Trails (4), MI	8	47.102, -88.554	5	4.9
Nara Trails (5), MI	9	47.106, -88.555	5	4.9
Maasto Hiihto (2), MI	30	47.140, -88.612	3	4.9
Blue Berry Ridge Trails, MI	14	46.456, -87.424	6	5.0
Mouth of the Huron River, MI	12	46.909, -88.036	6	5.4
Au Train, MI	15	46.438, -86.878	6	5.4
Big Bay de Noc, MI	16	45.868, -86.518	3	5.5
Cygnet, OH	28	41.238, -83.680	5	9.8
Warfordsberg, PA	27	39.737, -78.180	4	11.3
Hoosier, IN	18	38.060, -86.661	4	12.9
Trail of Tears, IN	21	37.480, -89.360	6	13.6
Rockwood Park, VA	29	37.451, -77.580	4	14.2

novel hybridizations is minimal (Pedlar et al. 2012, Ste-Marie et al. 2011). The populations selected for movement, should be selected based on their potential for handling a site's future climate (Jump and Peňuelas 2005, Krutovsky et al. 2012, Mátyás 2010). Provenance experiments can be used to categorize a population's phenotypic plasticity and environmental tolerance (Etterson et al., 2020, González-Martínez et al. 2006, Pedlar et al. 2012). In the case of the northern red oak, provenance studies often observed that seed stock from southern provenances are better adapted to changing climate in northern latitudes (Etterson et al. 2020, Kriebel 1976). To paraphrase Clark and Schlarbaum (2018), the best way to ensure the health of *Q. rubra* population is by planting a diverse stock of tree gathered from many populations.

To gain a better understanding of the *Q. rubra* populations' specific environmental tolerance, we designed two common garden sites that house 22 unique populations (Table 1). Biometric traits of all trees are routinely collected at these sites. Here we present the preliminary results relating to 2019 and 2020 biomass measurements and 2021 frost damage. We hypothesized that the response of each *Q. rubra* population to environmental site conditions would be largely dependent on a populations' seed-source climate variables.

METHODS

Quercus rubra Seed Collection and Germination

Quercus rubra inhabits forests spanning from southern Quebec and Ontario (Canada) to northern Louisiana (USA) and from the Mississippi River to the east coast of North America (Little 1971). Within this range, we collected seed stock from 22 distinctive populations (Table 1). Within each population, seeds were collected from multiple families. Approximately 50 acorns were directly sampled from the branches and immediate area surrounding the family's mother tree. Because *Q. rubra* is wind pollinated, all seeds collected from a single mother tree are half-siblings. After collection, the seeds were stored at 4 °C between 3 to 6 months for stratification (Bonner 2008).

After stratification, 20 seeds that passed the float/sink test from each family were randomly selected for germination at the Michigan Technological University College of Forest Resources and Environmental Sciences greenhouse. The acorns were individually planted into half-liter plugs filled with a soil/sand mix (75/25 percent) on April 3 and 4, 2019. Greenhouse conditions were maintained at 16-hour light and 8-hour dark periods. Day and night temperatures were maintained at 23 °C and 18 °C, respectively. Each of the half-liter plugs were saturated with water every 3 days. This period of greenhouse growth lasted approximately 3 months.

Common Garden Site Description and Design

Common garden sites are located at the Michigan State University W.K. Kellogg Experimental Forest (Augusta, MI; 42.47 N, -85.36 W) and the Michigan Technological University Ford Forest (Alberta, MI; 46.64 N, -88.48 W). The Kellogg site is considerably warmer and wetter than the Ford site. The mean annual temperatures are 9.9 °C and 4.9 °C, respectively; and yearly precipitation are 1027 mm and 879 mm, respectively. Site soil type is coarse sandy loam and loam, respectively (NRCS 2021).

The Kellogg and Ford common garden sites were established June 12 and June 19, 2019, respectively. At each common garden, 810 experimental red oak seedlings were arranged in rows with spacing of 1.5 m × 0.76 m. Each common garden site contains 27 blocks, consisting of 30 seedlings planted in 3 rows with 10 plants per row. The borders of each block are separated by buffer trees. Seedling locations were set using a semi-randomized block design (Dodge 2008). Each block contains at least one plant per population.

To prevent deer browsing, the perimeter of the common gardens is surrounded by 3 m high fences. To reduce the impacts of resource competition on the seedlings (e.g., light and nutrients), we employed regular weed management including lawn mowing, hand weeding, and herbicidal treatment, as needed. Plants at the Ford site were watered as necessary during the 2019 and 2020 growing seasons when dry conditions endangered seedling survival. To support root nutrient uptake, iron chelate was administered to all trees at the Ford common garden on August 12, 2019, and June 13, 2020.

Biometric Trait Assessment

Biometric traits were measured for all experimental plants in the common gardens. The biometric traits measured included seedling height (H), crown diameter (CD) measured in two directions, and stem diameter (SD). H measured the distance from a seedling's stem base to the terminal shoot tip, to the nearest centimeter. CD measured the distance from one side of the crown

through the central axis, to the nearest centimeter. To account for the lack of uniformity in crown growth, each seedling's CD was recorded for both horizontal and perpendicular directions (in reference to the rows and columns). SD was measured at the seedling root collar using calipers to 1/100 millimeter. Using these measurements, we calculated an aboveground biomass index (BI) for each seedling using the following formula:

$$\mathrm{BI} = \left(\frac{\mathrm{H} * \mathrm{CD1} * \mathrm{CD2}}{3} * \mathrm{SD}\right) * 1/1000$$

As an index, the BI is a unitless measurement meant to provide a way of comparing the seedlings.

Greenhouse measurements were used to approximate an initial BI measurement (BI-0) for the seedlings. The term "approximate" is used here because stem diameter measurements were not collected within this dataset as this could potentially damage the seedlings at this stage. All stem diameters are set at 1 mm, a value that is less than the smallest measurement in the first set of field measurements. To determine seedling growth between the common garden planting date and the end of the 2019 growing season, BI-0 values have been subtracted from the 2019 end-of-season BI (BI-2019). Similarly, the sum of BI-0 and BI-2019 were subtracted from the 2020 end-of-season BI to determine the BI-2020. The Ford site biometric trait data shown here was collected on August 27, 2019, and August 28, 2020. The Kellogg site biometric trait data shown here was collected on August 20, 2019, and August 13, 2020.

Frost Damage Assessment

In late May 2021, seedlings at the Ford site experienced multiple days of temperatures at or below freezing. At this time, most of the seedlings had gone through bud burst. We assessed the extent of frost damage through an index. Severity of frost damage was assigned a value between 0 and 3, where "0" indicated no frost damage and "3" indicated severe frost damage. The percentage of the seedlings that were afflicted with frost damage was assessed (approximated to be 0, 10, 25, 50, 75, 100 percent). The frost damage index was the product of severity and percentage. These data were collected on May 31 and June 1, 2020. Dormant seedlings were excluded from this analysis.

Statistical Analysis

A one-way ANCOVA was performed to determine if the common garden sites (Kellogg and Ford), seed source mean annual temperature (MAT), and site-MAT interaction had significant statistical effects on BI during the 2019 and 2020 growing seasons (i.e., BI ~ MAT*Site). Whisker boxplots of BI (2019 and 2020) by population were made to understand a population's BI distribution. A linear regression analysis was performed to determine if MAT had a significant effect on *Q. rubra* BI during the 2019 and 2020 growing seasons. Seedlings without leaves were excluded from these analyses since they could not be accurately assessed using our BI formula.

Since frost damage was only categorized at our Ford common garden site, we performed a linear regression to determine if MAT had significant effect on *Q. rubra* frost damage in 2021. Whisker boxplots of the frost damage index by population were made to compare data distribution for each population. Dormant seedlings were excluded from this analysis.

RESULTS

Seed Source Mean Annual Temperature and Site have a Significant Effect on *Quercus rubra* Seedling Above Ground Biomass Index

In both 2019 and 2020 growing seasons, we observed significant effects of seed source MAT and common garden site on *Q. rubra* aboveground biomass index. The average biomass index for *Q. rubra* populations was greater at the Ford common garden site in 2019. A similar trend was observed during the 2020 growing season (Table 2, Fig. 1). Although no interactive effect between seed source MAT and common garden site was observed in 2019, we did observe an interactive effect in 2020 (Table 2).

Table 2.—Effects of seed source mean annual temperature and site on *Q. rubra* biomass production and frost damage. One-way ANCOVA used for BI 2019 and BI 2020 data, and linear regression for FD 2021 data (for Ford common garden only). Statistically significant p-values are in bold. BI: biomass index; DF: degrees of freedom; FD: frost damage; MAT: seed source mean annual temperature.

Source	BI 2019		BI 2020		FD 2021	
	DFn/DFd	p	DFn/DFd	p	DFn/DFd	p
MAT	1/1086	**<0.001**	1/1006	**<0.001**	1/614	**<0.001**
Site	1/1086	**<0.001**	1/1006	**<0.001**	NA	NA
MAT*Site	1/1086	0.576	1/1006	**0.011**	NA	NA

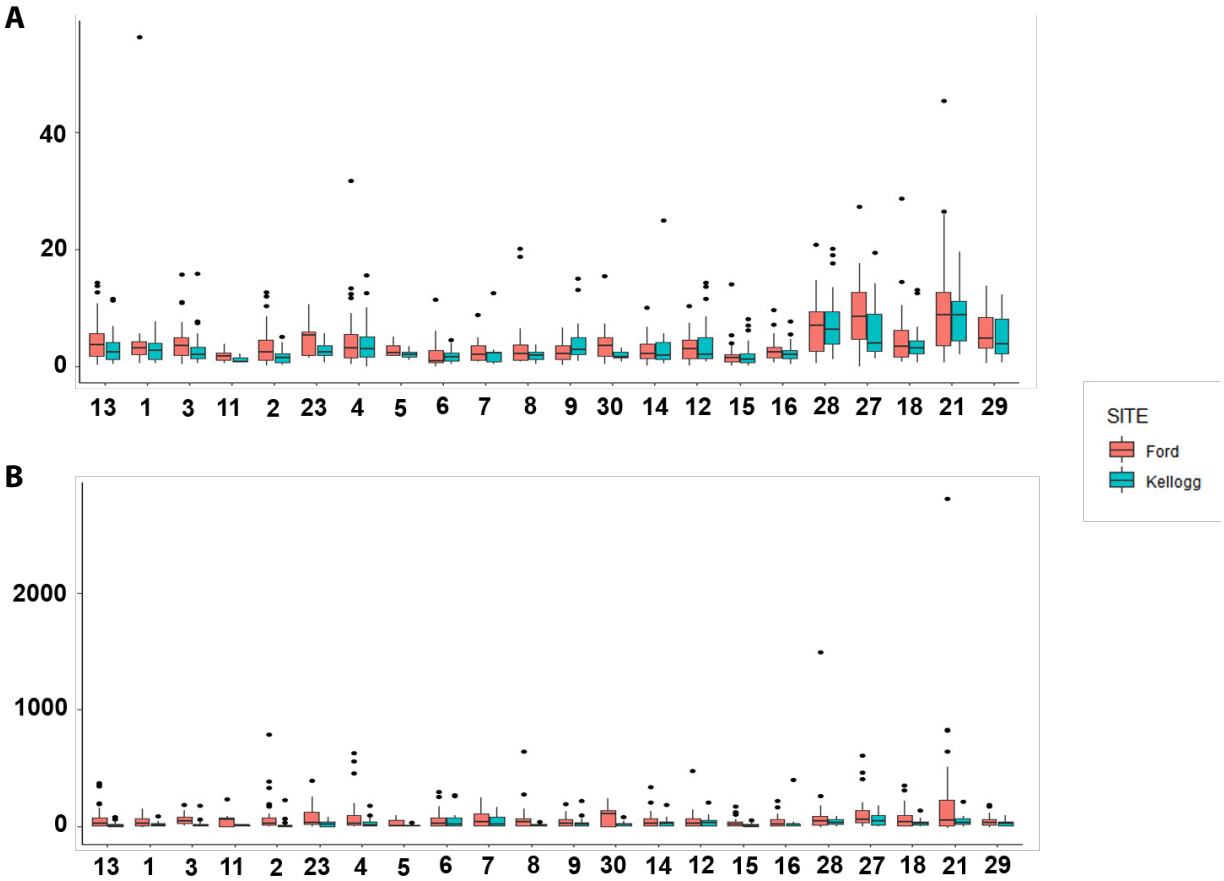

Figure 1.—Biomass indexes for *Q. rubra* provenances. Provenances are ordered based on seed source MAT, from lowest to highest. Ford site boxplots are red; Kellogg site boxplots are blue. (A) 2019 biomass indexes, and (B) 2020 biomass indexes.

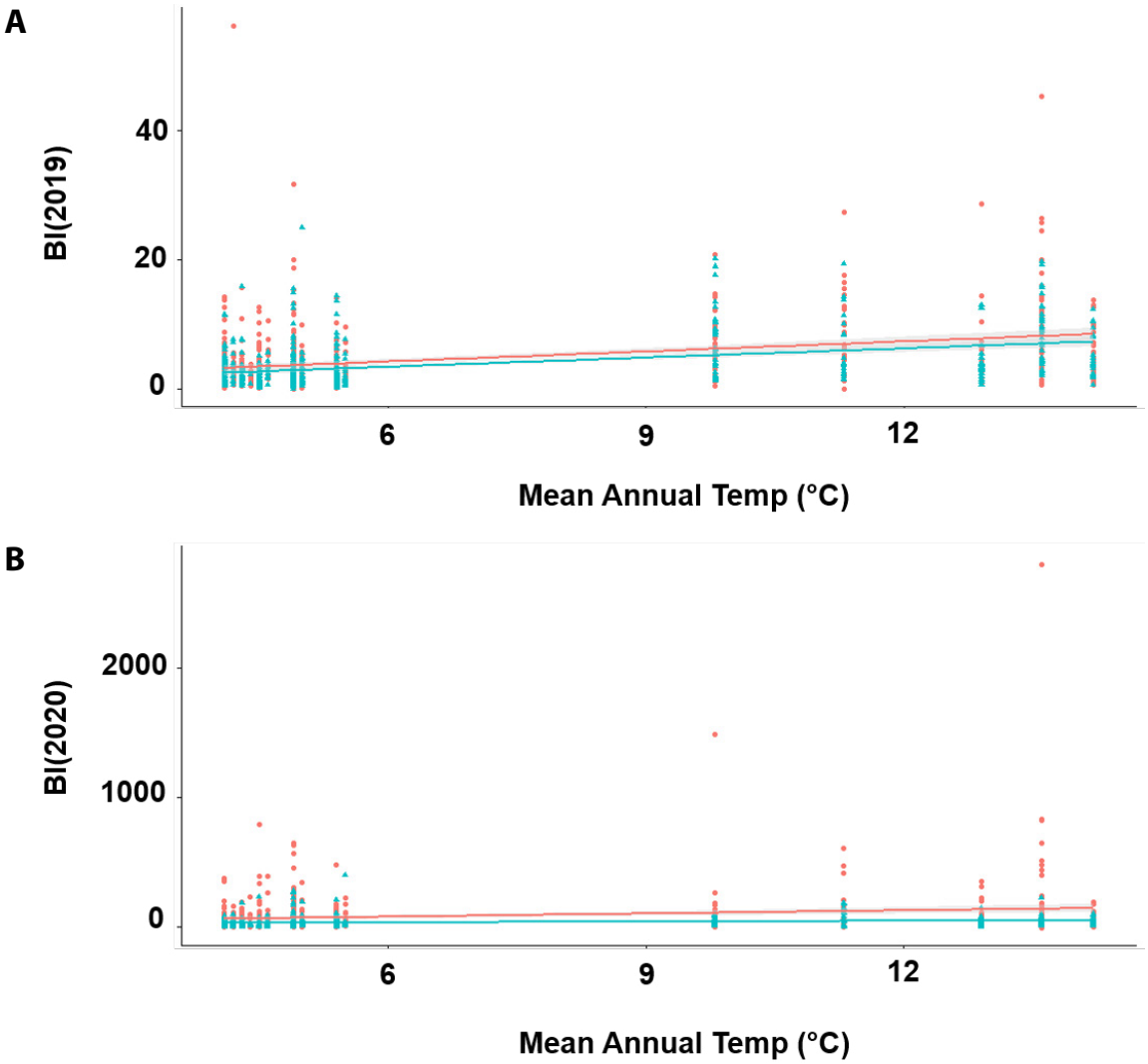

Figure 2.—Positive correlations observed for linear regressions of *Q. rubra* biomass index (BI) with respect to seed source mean annual temperature (MAT). Ford site data are orange circles; Kellogg site data are teal triangles. (A) 2019 biomass indexes with respect to MAT: Ford site β0, β1, R2, and p-values are 1.037 BI, 0.388 BI/°C, 0.078, and <0.001, respectively. (B) Kellogg site β0, β1, R^2, p-values are 0.570 BI and 0.327 BI/°C, 0.114, and <0.001, respectively. 2020 biomass indexes with respect to MAT (B): Ford site β0, β1, R2, and p-values are 25.672 BI, 8.151 BI/°C, 0.026, and <0.001, respectively; Kellogg site β0, β1, R2, and p-values are 18.814 BI and 1.979 BI/°C, 0.024, and <0.001 respectively.

We observed a strong, positive correlation between *Q. rubra* aboveground biomass and seed source MAT at both common garden sites during 2019 and 2020. Similar linear regression equations describe correlation between MAT and BI at both the Kellogg (Y = 0.327BI/MAT * X + 0.570BI) and the Ford (Y = 0.388BI/MAT * X + 1.037BI). In 2020, we found the slope of the Ford site regression line to be more than four times greater than that of the Kelogg site regression. The linear regression equations Y = 8.151BI/MAT * X + 25.672BI, and Y = 1.979 * X + 18.813BI, respectively, describe the trends observed at the Ford and Kellogg sites (Fig. 2). Low R^2 values were found for each regression analysis, demonstrating that MAT only explains some of the variability of the biomass index means. Significant p-values were found for each of the linear regressions, demonstrating that MAT has a significant effect on biomass production at both common garden sites (Fig. 2).

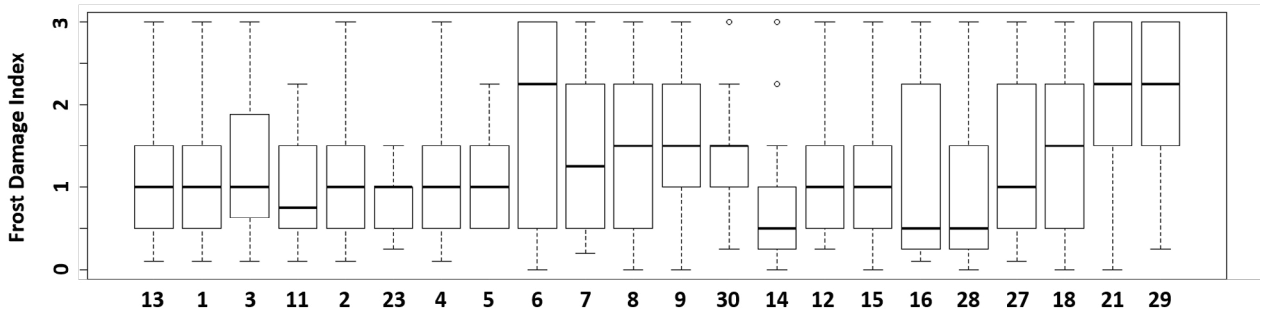

Figure 3.—2021 frost damage index boxplots for *Q. rubra* provenances at the Ford common garden. Provenances are ordered based on seed source mean annual temperature, from lowest to highest.

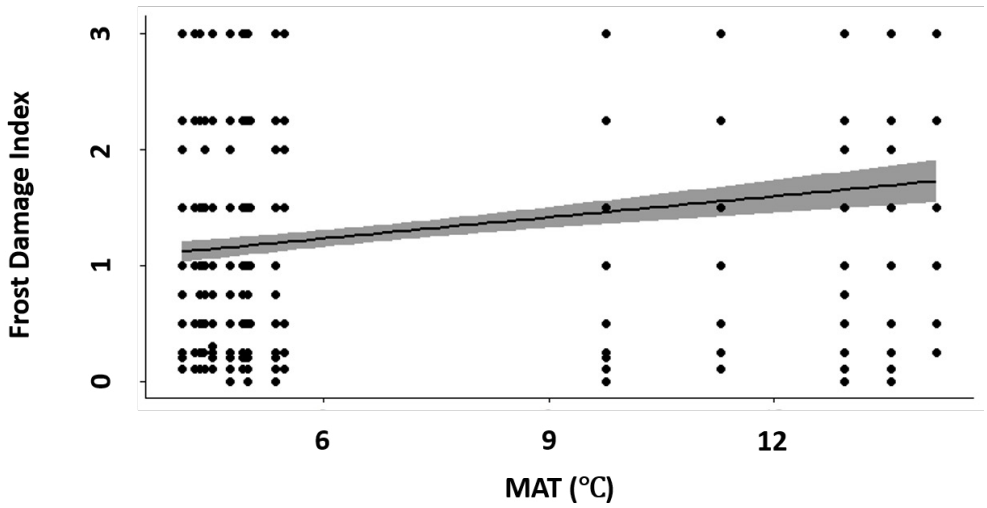

Figure 4.—Positive correlation observed for linear regression of *Q. rubra* frost damage with respect to seed source mean annual temperature (MAT) at the Ford common garden. β0, β1, and R^2 values are 0.87 FD, 0.06 FD/°C, and 0.044, respectively.

Seed Source Mean Annual Temperature had a Significant Effect and a Positive Correlation on *Quercus rubra* Seedling Frost Damage

Linear regression analysis found seed source MAT has a significant effect on the degree of frost damage experienced by *Q. rubra* seedlings (Table 2). The boxplot analysis of these data shows the wide distribution of the frost damage index within and between each *Q. rubra* population (Fig. 3). Our regression analysis helps explain the differences between the provenances, revealing a significant, positive correlation between the degree of frost damage sustained and the seed source MAT of the *Q. rubra* seedlings (Fig. 4). A low R^2 value was found for this regression analysis (Fig. 4), demonstrating that seed source MAT explains a small amount of the variability for the frost damage index.

DISCUSSION AND CONCLUSIONS

In our initial hypothesis, we stated that the response of the *Q. rubra* population to environmental and site conditions would be dependent on the provenance seed source climate variables. This hypothesis is based on the principal that ecological selective pressures influence a population's genetic structure within a species (Lowe 2017). Results from a previous study conducted by Etterson et al. (2020) support our initial hypothesis. Their provenance study, which investigated the performance of Minnesotan *Q. rubra* populations using a common garden located in the northern edge of the species' range, found that the southern populations showed greater survival and growth when compared to their northern counterparts (Etterson et al. 2020).

Our ANCOVA analysis of *Q. rubra* seed source MAT and aboveground biomass index revealed findings similar to Etterson et al. (2020) and supported our initial hypothesis. At both common garden sites, during both the 2019 and 2020 growing seasons, we found that *Q. rubra* estimated aboveground biomass (reported by the BI values) increased with the increasing seed source MAT (Fig. 2). We found that populations collected from the southern regions of the *Q. rubra* range, the provenances with warmer seed source MAT, such as populations 18, 21, 27, 28, and 29, had on average greater biomass (Figs. 1, 2 and Table 1). This demonstrates that in the absence of late spring or early fall frosts, we observe faster growth of *Q. rubra* from southern provenances grown in northern latitudes.

During the 2020 growing season, our linear regression analysis of seed source MAT and biomass found a four times steeper slope at the Ford common garden site (Fig. 2B). When comparing the data distribution between the populations, we found that the biomass averages for a population are greatest at the Ford common garden site in 2020 (Fig. 1B), a result similar to what has been reported by Etterson et al. (2020).

Assisted migration is a forest management tool for adapting an existing population to future climate change conditions by the intentional introduction of foreign seed stocks (Minteer and Collins 2010, Pedlar et al. 2012). Often, this form of assisted migration involves the movement of southern provenances into the northern range or leading edge of the current species range. This is intended to add to an existing provenances climate change resilience. However, movement of population genotypes that are not matched with the growing patterns of an established population could increase the existing populations risk for frost damage (Aitken and Hannerz 2001). Thus, forestry assisted migration needs to strike a balance between maximizing a population's growth under climate change and limiting injury caused by late spring or early fall frosts (Schreiber 2013). From our initial hypothesis, we would predict that *Q. rubra* populations with greater seed source MAT would experience a greater degree of frost damage. Our regression analysis of the 2021 frost damage revealed that the degree of damage sustained is positivly correlated to a populations seed source MAT (Fig. 4). The populations 6, 21, and 29 had the highest frost damage index (Fig. 2, Table 1). The degree of frost damage sustained by populations 21 and 29 is supportive of our initial hypotheis, since these populations were collected from our southern-most sites and had the highest seed source MATs. A higher frost damage index was observed for population 6, an interesting result compared to other populations within the same provenance (Nara Nature Park trail, Houghton, MI: populations 5, 6, 7, 8 and 9). Although this population had a similar mean frost damage index to populations 21 and 29, the lower quartile of population 6 shows is considerably lower then these southern populations (Fig. 3).

With regards to frost damage and assisted migration, studies of growth optimization versus survival optimization have already been investigated for some tree species. Schreiber et al. (2013) found that the northward migration of trembling aspen (*Populus tremuliodes*) only sightly delayed growth for southern provenances. Their study concluded that assisted migration of southern trembling aspen provenances to the northern latitudes had either postitive or neutral effects on a population growth and survival. Their results hightlight a need for future experiments investigate if frost damage has a greater effect on *Q. rubra* provenance growth and survival.

The data we present here complements studies such as Kriebel et al. (1976), Etterson et al. (2020), and Leites et al. (2019) and helps to understand the physiological and growth responses of oak provenances in common garden experiments. Results such as these are necessary to make informed decisions on forestry assisted migration, which may soon be the norm to save populations or entire species from anthropogenic-caused extinction.

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