

Article

Climate Adaptation in White Oak (*Quercus alba*, L.): A Forty-Year Study of Growth and Phenology

Austin M. Thomas ^{1,*} , Mark V. Coggeshall ^{2,3}, Philip A. O'Connor ⁴ and C. Dana Nelson ^{5,6,*} 

- ¹ Oak Ridge Institute for Science and Education (ORISE), Forest Health Research & Education Center, Southern Research Station, USDA Forest Service, Lexington, KY 40546, USA
- ² School of Natural Resources, University of Missouri, Columbia, MO 65211, USA; coggeshallm@missouri.edu
- ³ Hardwood Tree Improvement and Regeneration Center, Northern Research Station, USDA Forest Service, West Lafayette, IN 47907, USA
- ⁴ Vallonia Tree Seedling Nursery, Indiana Division of Forestry, Vallonia, IN 47281, USA; poconnor@dnr.in.gov
- ⁵ Forest Health Research & Education Center, Southern Research Station, USDA Forest Service, Lexington, KY 40546, USA
- ⁶ Southern Institute of Forest Genetics, Southern Research Station, USDA Forest Service, Saucier, MS 39574, USA
- * Correspondence: austin.thomas@uky.edu (A.M.T.); charles.d.nelson@usda.gov (C.D.N.)

Abstract: Climate change poses a significant threat to the resilience and sustainability of forest ecosystems. This study examines the performance of white oak (*Quercus alba*, L.) across a range of provenances in a common garden planting, focusing on the species' response to climatic variables and the potential role of assisted migration in forest management. We evaluated the survival and growth rates of white oak provenances originating from various points along a latitudinal gradient over a period of 40 years. These provenances were planted in a common garden situated near the midpoint of this latitudinal gradient, where we also monitored their phenological traits, such as budburst and leaf senescence. The results revealed substantial variation in phenological responses and growth patterns among the provenances, with southern provenances demonstrating faster growth and later senescence relative to local sources, with limited impact on survival. In contrast, the northern provenances demonstrated slower growth, resulting in later-aged competition-induced mortality. The findings highlight the necessity of incorporating genetic diversity into white oak reforestation and conservation strategies, as the local provenance may no longer be the most suitable option for current and future conditions. We advocate for a nuanced approach to forest management that leverages genetic insights to optimize seed source selection for reforestation, fostering resilient forest landscapes in the face of ongoing climate shifts.

Keywords: white oak; *Quercus alba*; provenance test; common garden; phenology; assisted migration; climate change; tree growth



Citation: Thomas, A.M.; Coggeshall, M.V.; O'Connor, P.A.; Nelson, C.D. Climate Adaptation in White Oak (*Quercus alba*, L.): A Forty-Year Study of Growth and Phenology. *Forests* **2024**, *15*, 520. <https://doi.org/10.3390/f15030520>

Academic Editors: Yassine Messaoud, Jan Světlík and Giorgio Alberti

Received: 30 December 2023

Revised: 4 March 2024

Accepted: 4 March 2024

Published: 12 March 2024



Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

White oak (*Quercus alba*, L.) is an iconic deciduous tree prevalent throughout the hardwood forests of the eastern United States, extending from Maine to Florida and from Minnesota to Texas [1,2]. Although capable of thriving in diverse soils, it exhibits a particular preference for well-drained loamy soils that offer moderate moisture and fertility [2,3]. Throughout its range, this species is a key component of various forest types, including oak-hickory, oak-pine, and mixed hardwoods [4,5]. As a keystone species, white oak provides essential ecosystem services, playing a pivotal role in carbon sequestration, oxygen generation, and water purification, all while forming the basis of intricate multi-trophic systems [5]. The resilience of white oak is exemplified by its longevity [6]. However, recent evidence suggests a concerning decline in white oak populations within eastern forests attributed to overharvesting, high grading, inconsistent regeneration, and poor recruitment [7–9].

The genus *Quercus* includes approximately 435–500 oak species native to temperate and subtropical regions [10,11]. Among these, white oak stands out as the most preferred of only three oak species widely used in liquid goods cooperage [11]. Its robust and durable heartwood is particularly prized for crafting bourbon barrels, which are subsequently repurposed in the production of other whiskeys and wine [12]. Given the commercial and ecological value of white oak, coupled with its regional decline [7], there is growing interest among federal, state, and private entities in white oak reforestation and tree improvement [13–15]. Despite the genus *Quercus* being known for its adaptability to environmental variation [16], such plasticity in white oak, specifically, has not been thoroughly investigated.

In light of ongoing global climate change, the consideration of both phenotypic and genetic factors influencing white oak performance is crucial. Assisted migration, and more specifically assisted population migration, i.e., the transfer of seeds from the southern part of a species' geographical range to the north (in the northern hemisphere) [17], is regarded as one way to assist a species' adaptation to global warming. Traditional forestry practices advocate for the use of local seed sources that are presumed to be well adapted to local conditions. However, these notions are challenged by ongoing rapid environmental changes, suggesting that southern genotypes might be better suited for northern locations in the future due to their adaptation to warmer climates [18]. Economically important forest tree species, especially those with large geographical ranges, often have ecotypes or substantive clines adapted to local site conditions. The phenotypic and genetic intraspecific variation of forest trees in the context of assisted migration have been less studied than interspecific variation and competition [19].

A comprehensive understanding of white oak's response to climatic variables over its lifespan is necessary for delineating seed zones and guiding assisted migration strategies in the context of climate change. The majority of eastern hardwood species are primarily experiencing a southern range retraction with evidence of a significant lag between temperature shifts and northward migration [20]. Dispersal models of white oak indicate that unassisted, the species' natural distribution will lag significantly behind the northward shift of the species' suitable climate envelope [21]. If white oak lacks the plasticity to adapt to rapid climate warming, then the assisted northward range expansion and population migration of provenances northward may be necessary to avoid substantial range retraction exacerbated by the species' particularly long life and limited natural dispersal abilities [22].

In this study, we investigate the survival, growth, and phenological traits of white oak provenances growing in a common garden planting. While provenance performance is ideally assessed at multiple planting sites with varying environmental conditions, this study's scope is confined to a single common garden near the center of the species range. We acknowledge conclusions drawn from this research must be made with caution but believe there is a pressing need for the quantitative assessment of white oak provenance performance. This common garden study represents, to the best of our knowledge, the only long-term investigation incorporating white oak genetics representative of most of the latitudinal range of the species, the foremost requirement of a provenance study [23]. Our analysis spans 40 years of tree growth measurements and increment core records complemented by spring leaf budburst and fall leaf senescence data collected in years 39 and 40. We used these phenology data to estimate the length of the growing season for each provenance under the contemporary climate conditions at the planting site.

We expected that the white oak provenances in this study would exhibit distinct growth, survival, and phenological responses to the environmental conditions at our common garden site. We predicted high mortality in the Mississippi provenance due to late spring and early fall freezes, and potential slower growth in northern provenances. These hypotheses reflected our anticipation of latitudinal influences on provenance performance. Some of our hypotheses were confirmed by the study outcomes, while others were contradicted by the data. Analyzing the growth and phenological traits of white oak seed source origins spanning a range of climatic conditions, this study underscores the critical role of

adaptive genetic management in forest conservation, providing invaluable insights for tree breeders and forest managers as they navigate the challenges posed by climate change.

2. Materials and Methods

Two-year-old bare root seedlings grown at the Vallonia Nursery (Indiana Department of Natural Resources, Vallonia, IN, USA) were planted in 1983 at the Starve Hollow State Recreation Area on a site 2 km from the nursery. The common garden experiment was planted on level terrain, situated 180 meters north of Starve Hollow Lake, in the well-drained sandy-loam soils characteristic of the Bloomfield-Alvin complex [24]. The seedlings represented six distinct provenances, including southern Minnesota (MN), southern Wisconsin (WI), central Ohio (OH), southern Indiana (IN), southern Illinois (IL), and northern Mississippi (MS). Detailed coordinates, seed source information, and climate summaries for each provenance are provided in Table 1 and Figure 1. The selection of seed source locations was guided by two primary considerations. Firstly, an effort was made to ensure that these locations spanned the latitudinal range of white oak, with the intent of capturing most of the species' genetic diversity as it relates to climate adaptation represented by plant hardiness zones [25]. However, the predominant consideration, given the nature of white oak's recalcitrant seeds, was the location of accessible acorns in the fall of 1981 and the availability of a suitable planting site.

The common garden planting was arranged in a 12 row by 18 column grid ($n = 216$) with 2.5 meter tree spacing. This grid was divided into six randomized complete blocks, each containing nine four-tree row plots. Some provenances contained more than one plot (see Table 1). The southern Indiana seed sources were collected from two locations 100 km apart, each of which were planted in their own plot. Given their similar latitude and proximity, both Indiana sources were treated as a single provenance (IN) in our analysis. The southern Illinois seed sources consisted of three open pollinated families, coming from a single location, each of which were planted in their own plots. We also treated these Illinois sourced plots as a single provenance (IL) for the purposes of our analysis. A one-tree border row was planted around the whole experiment with a local seed source. The experiment was thinned in year 12, halving the number of trees in each plot ($n = 108$ after thinning) to reduce tree-tree competition within and between plots. Tree mortality (natural and via thinning) was tracked throughout the study. Local tree density (number of orthogonal and diagonal neighbors) was included as a cofactor in all statistical models to account for the effects of neighbor-tree competition and canopy gaps left by tree mortality or thinning.

Table 1. Coordinates in decimal degrees and the USDA Plant Hardiness Zones [25] of provenances planted in the common garden study located near Vallonia, Indiana (latitude = 38.82, longitude = −86.08, elevation = 174.04 m).

Prov.	Lat.	Long.	Elev. (m)	USDA Zone 1990	USDA Zone 2023	Mother Trees per Prov.	Plots per Block	State	County	Place Name
MN	45.00	−93.10	256.34	4a	5a	10	1	Minnesota	Ramsey	University of Minnesota campus
WI	43.00	−89.30	269.44	4b	5a	10	1	Wisconsin	Dane	Nevin State Fish Hatchery
OH	40.28	−84.10	272.00	5a	6a	6	1	Ohio	Auglaize	Wapakoneta Fairgrounds
IN	39.06	−86.59	176.78	5a	6a–6b	6	2	Indiana	Greene, Jackson	Shakamak State Park, Vallonia Tree Seedling Nursery
IL	37.40	−89.13	183.25	6a	7a	3	3	Illinois	Jackson	Private residences in Makanda
MS	34.37	−88.36	120.40	7b	8a	8	1	Mississippi	Prentiss	Private residences south of Booneville

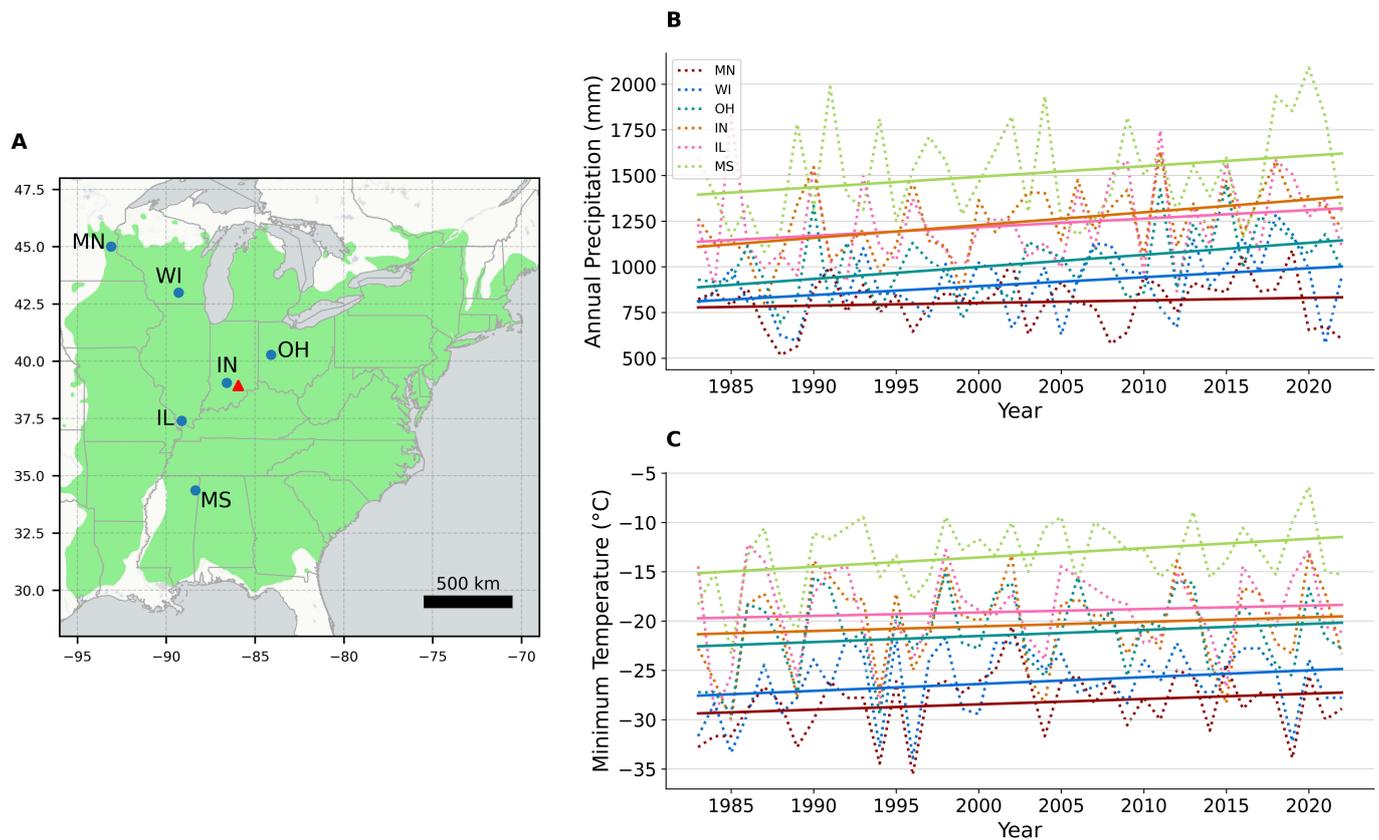


Figure 1. Locations of seed source origins and relevant climate information for each provenance. (A) Map of provenance locations. Solid gray lines indicate US state and Canadian provincial borders. Green shading indicates the natural range of white oak (*Quercus alba*, L.) [1]. Provenances are represented as labeled blue dots. The location of the common garden in southern Indiana is represented as a red triangle. (B) Annual precipitation (mm) of each provenance [26]. Solid lines represent the linear trend of each provenance with the corresponding color. (C) Annual mean absolute minimum temperatures (°C) of each provenance [26]. Again, solid lines represent the linear trend of each provenance with the corresponding color. The Indiana provenance and test location data are based on regional climate data covering both seed source locations and the common garden site.

Diameter at breast height (DBH, approximately 1.3 m) was measured to the nearest 0.1 inches (2.54 mm) in the 11th, 20th, and 40th years using a diameter tape. Annual DBH estimates were derived from two 5.15 mm diameter increment cores extracted from each tree in early spring 2022, oriented east-west and north-south, respectively, and taken as close to breast height as possible while avoiding any epicormic branching. Increment cores were mounted on poplar blocks and sanded smooth before precision dendrochronological measurements were made using a Velmex TA measurement system (Velmex, Inc., Bloomfield, NY, USA). The average radial growth from these two cores was calculated, adjusted for average bark thickness, and multiplied by two to represent annual DBH growth. These measurements were analyzed using nonlinear modeling to evaluate growth differences between provenances, employing the ‘nlme’ package in R [27,28]. Cumulative DBH growth curves were fit using the Schumacher growth model [29,30] (Equation (1)), where a = the growth asymptote, b = the growth scale factor, and x = the year.

$$y = a * e^{-b\frac{1}{x}} \quad (1)$$

The height of each tree was measured at the time of planting (year 0) as well as in the fall of years 1–5, year 20, and year 40. The height of trees in years 0–5 was measured via a measuring rod to the nearest cm, and in years 20 and 40 via a Forestry Pro II hypsometer

(Nikon, Minato, Tokyo) to the nearest 0.1 ft (3.048 cm). Again, a nonlinear model was used to discern statistical differences across provenances. Height growth curves were fit via the 3P Gompertz growth model (Equation (2)), where a = the growth asymptote, b = x-axis displacement (translation along the x-axis), c = the growth rate, and x = the year.

$$y = a * e^{-bc^x} \quad (2)$$

Phenological observations of spring leaf budburst were recorded in 2022 (year 39) and 2023 (year 40). Canopies were visually sectioned into thirds (lower, middle, and upper), and leaf budburst was assessed for each section using a 0–6 point scale, adapted from Cole and Sheldon’s seven-stage key for oak bud development [31] on a roughly weekly basis. Leaf scores grouped by provenance were then analyzed via a linear mixed model. The date at which half of the trees reached a score of ≥ 3 was established as the onset of the growing season for each provenance (50% of trees at 50% budburst or greater). Celsius growing degree days (GDDs ($^{\circ}\text{C}$)) corresponding to the date of season start of each provenance were calculated using a base temperature of 10°C and method one described by McMaster and Wilhelm [32,33].

Fall leaf senescence observations were made in the fall of 2022. Estimates of the percentage of brown (marcescent) or abscised (senescent) leaves in each tree canopy were made on a roughly weekly basis. A nonlinear model was used to discern statistical differences across provenances, fitting each provenance to a modified 4P logistic model (Equation (3)) where a = the point of inflection, b = Hill’s slope, and x = the date.

$$y = \frac{1}{1 + e^{\frac{a-x}{b}}} \quad (3)$$

Peak senescence intensity, defined by the PhenObs initiative as 50% of leaves fully brown or abscised [34], was established as the end of the growing season for each provenance. The length of growing season was calculated by summing the number of days between growing season start and growing season end.

3. Results

The DBH growth model revealed significant differences among the six white oak provenances planted in the common garden experiment ($p < 0.01$, Figure 2). In general, maximum DBH was greater in the southern provenances, with the Mississippi provenance (MS = 42.98 cm) exhibiting the highest growth asymptote (Figure 2B). The Wisconsin provenance appeared to be an outlier, underperforming compared to even the Minnesota provenance (WI = 29.55 cm, MN = 37.69 cm), which originated further north (Table 1). However, several Wisconsin trees suppressed in the understory are likely to die in the near future, whereas the Minnesota-sourced trees that were suppressed had all died by year 40, persisting only as partially decayed snags or stumps. As all surviving trees were used in the analysis, this may account for the outlying low DBH growth performance of the Wisconsin provenance. Minnesota and Ohio sourced trees had a notably greater Schumacher scale factor than the other provenances, indicating slower early growth than other provenances in the study (Figure 2C).

The height growth model also revealed significant differences among the six white oak provenances ($p < 0.01$, Figure 3). The Indiana and Illinois provenances reached the greatest heights (IN = 26.04 m, IL = 26.03 m), although the Mississippi-sourced trees were nearly as tall (24.68 m). There were no significant differences in the x-axis displacement parameter between provenances, and height growth started immediately for all sources, indicating that there was no delay due to transplant shock or unfavorable site factors.

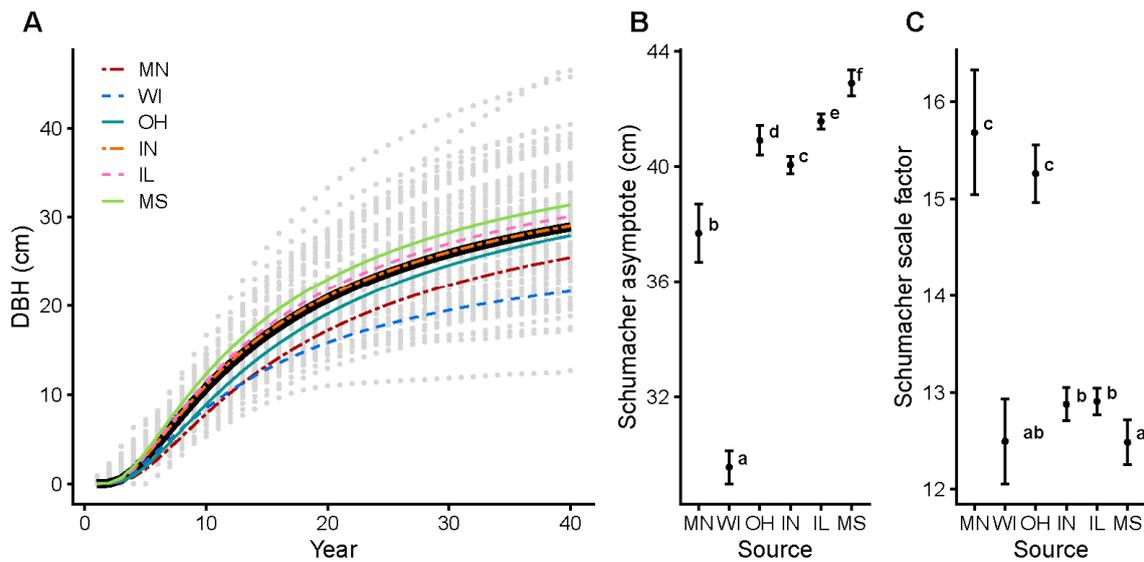


Figure 2. Summary of DBH growth (cm) of the six provenances planted in the southern Indiana common garden experiment ($n = 81$). DBH was reconstructed from increment cores and regular DBH measurements over the 40-year study period. (A) Schumacher growth model fits representing the mean DBH growth of each seed source. The solid black line represents the total population fit. (B) Connecting letters diagram (CLD) of the Schumacher asymptote parameter. Gray dots represent DBH measurement values. (C) CLD of the Schumacher scale factor parameter. For all CLDs, means not sharing any letter are significantly different at $\alpha = 0.05$ according to a Holm-Bonferroni corrected post-hoc test.

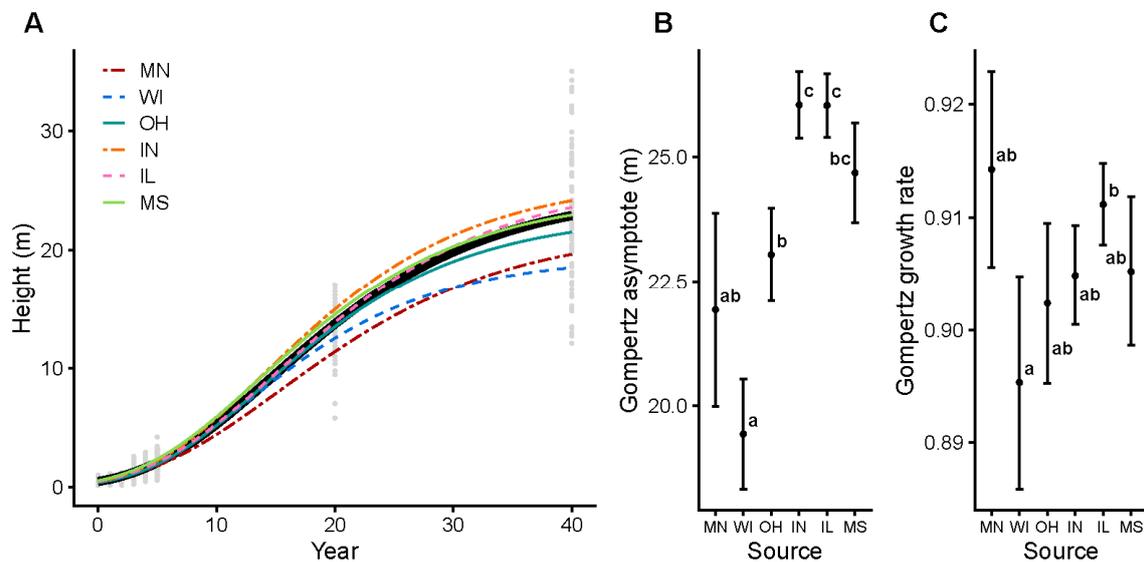


Figure 3. Summary of height growth (m) of the six white oak provenances planted in the southern Indiana common garden experiment based on regular height measurements over the 40-year study period ($n = 81$). (A) 3P Gompertz growth model fits representing the mean height growth of each provenance. The solid black line represents the total population fit. Gray dots represent height measurement values. (B) Connecting letters diagram (CLD) of the 3P Gompertz asymptote parameter. (C) CLD of the 3P Gompertz growth rate (y-scaling) parameter. For all CLDs, means not sharing any letter are significantly different at $\alpha = 0.05$ according to a Holm-Bonferroni corrected post-hoc test. Note that the post-hoc test for parameter b (x-axis displacement) is not shown as there were no significant differences between provenances.

The Gompertz growth rate parameter tracks inversely with growth, meaning a lower Gompertz growth rate parameter corresponds to a relatively steeper growth curve, although this is attenuated by the asymptote parameter. Growth rate parameters varied, with the Illinois and Minnesota provenances having the highest growth rate values (IL = 0.91, MN = 0.91). Thus, these provenances experienced relatively slower early height growth rates, but appeared to maintain their initial growth rate for longer (year ~15 to ~25) than the other provenances.

Linear mixed model analysis indicated a uniform onset of budburst across all provenances in the spring of 2022, as depicted by the closely clustered provenance mean scores in Figure 4A, and the lack of significant differences between provenances in the post-hoc comparisons in Figure 4B. This suggests a synchronous phenological response to springtime cues. However, spring conditions in 2022 were very atypical, with colder than average April temperatures (2.11 °C below 1980–2023 mean temperatures) and a very wet May (5.9 cm above average precipitation, ~150% of the norm; also more than 5.0 cm above the average May rainfall of all provenance seed origins) [35,36]. Due to the abnormal spring weather conditions in 2022, spring budburst was measured again in the spring of 2023, when seasonal conditions were much closer to the area's long-term averages.

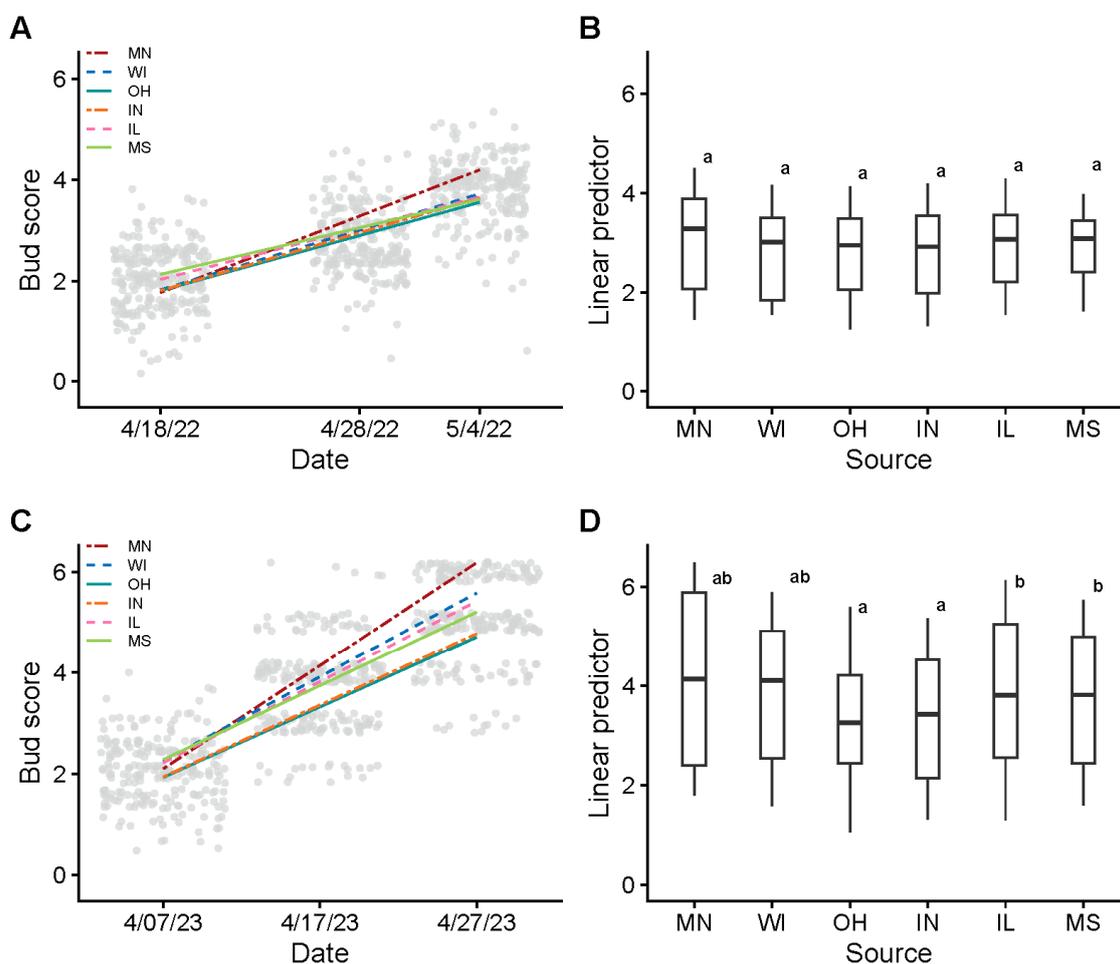


Figure 4. White oak budburst for each provenance planted in the southern Indiana common garden experiment. (A,C) Budburst scores over time for the six provenances during the spring seasons of 2022 and 2023, respectively ($n = 81$). Each gray point represents an individual tree's budburst score, and the lines indicate the average trend for each provenance. (B,D) Post-hoc analysis of the linear mixed models for the two years, presented as Tukey's HSD tests. For all connecting letters diagrams, means not sharing any letter are significantly different at $\alpha = 0.05$.

The 2023 budburst score data illustrates a departure from the previous year’s uniformity. Figures 4C,D reveal discernible variations in the budburst scores among the provenances. The Indiana and Ohio provenances, the sources closest in latitude to the common garden site, were more conservative than the more northern and the more southern provenances. Despite a statistically significant difference in budburst progression among provenances, this difference only accounts for a four-day difference (when rounding to the nearest 24-h period) in growing season start date (Table 2).

Table 2. Survival rates and estimated growing season length of white oak seed sources planted in the southern Indiana common garden experiment based on 2022/2023 bud scores and 2022 leaf senescence. Note that 11-year survival rates were measured prior to stand thinning at the end of year 12, while 40-year survival rates were measured after stand thinning.

State	Latitude	11 yr. Survival	40 yr. Survival	Season Start	Growing Degree Days (°C)	Season End	Season Length (Days)
MN	45.00	100%	25%	4/11	83.9	10/6	178
WI	43.00	96%	50%	4/11	83.9	10/13	185
OH	40.28	96%	92%	4/15	111.4	10/20	188
IN	39.06	94%	96%	4/14	101.9	10/20	189
IL	37.40	94%	89%	4/11	83.9	10/18	190
MS	34.37	100%	83%	4/10	81.9	10/23	196

Differences in the progression of fall leaf senescence were much more pronounced between seed sources (Figure 5A) than differences in spring budburst scores. Trees of more northern provenance lost their leaves significantly earlier than southern provenance trees (Figure 5B). Also notable was the timespan over which senescence occurred, with the most locally sourced trees (Indiana and Ohio) having lost their leaves over a much shorter period compared to more southern and northern provenances (Figure 5C).

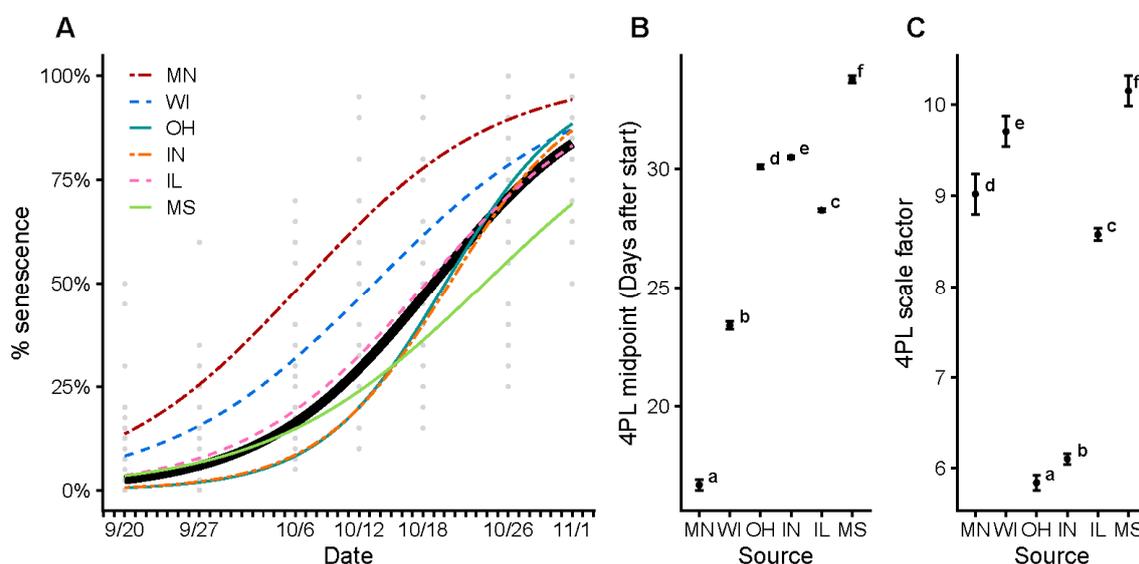


Figure 5. Summary of fall percent senescence, measured in fall 2022, for each of the six white oak seed sources growing in the southern Indiana common garden experiment ($n = 81$). Although based on the 4P logistic growth model, the start parameter was fixed at 0%, and the asymptote parameter was set at 100% for all provenances. (A) Model fits. The solid black line represents the total population fit. Gray dots represent the senescence score of individual trees. (B) Connecting letters diagram (CLD) of the 4P logistic midpoint parameter. (C) CLD of the 4P logistic scale factor parameter. For all CLDs, means not sharing any letter are significantly different at $\alpha = 0.05$ according to a Holm-Bonferroni corrected post-hoc test.

Differences between the estimated growing season length for each provenance were driven primarily by fall senescence due to the greater variability in fall phenology: a spread of 17 days vs. only four days in the spring (Table 2). Thus, the total estimated season length was greatest in the southernmost provenance of Mississippi (196 days) and shortest in the northernmost provenance of Minnesota (178 days), with a difference in length of 18 days. Over the course of the 40-year study, that equates to an ‘extra’ 720 days (or about four growing seasons) worth of growth in Mississippi provenance trees compared to Minnesota-sourced trees.

The provenance survival rate prior to thinning the stand at 11 years was close to 100% across all seed sources (Table 2). However, after 40 years of growth, a 50% and a 75% mortality rate (not including thinned trees) were observed in Wisconsin and Minnesota provenances, respectively (Table 2). This may be due in part to their slower growth and lesser competitive ability at this relatively southern site compared to the more southern provenances caused by their shorter effective growing season, among other potential maladaptive traits. Perhaps most surprising is the relatively low mortality (<20%) of Mississippi provenance trees after 40 years despite being planted in a climate that experiences regular hard freezes, which are relatively uncommon in Mississippi.

4. Discussion

Overall, white oak seedlings responded well to the plantation setting in southern Indiana, with no evidence of transplant shock or delayed growth. White oak provenances significantly influence phenological responses such as leaf budburst and leaf senescence, which are critical to the adaptive capacity of the species. The variation in growth performance and survival rates among provenances, particularly the superior growth observed in southern provenances like Mississippi, aligns with the concept that genetic selection for climate resilience could bolster forest health and productivity [37]. Furthermore, the low mortality of the Mississippi and southern Illinois provenances should assuage fears of ‘overshooting’ the climate envelope as these southern seed sources are already resilient to freezing conditions.

Some aspects of local provenances remain distinct from both more northern and more southern seed sources, but it is not clear if these traits impart a selective advantage. The spring phenology of the Indiana and Ohio provenances was slightly more conservative than both the northern and the southern provenances in 2023, although budburst was only postponed by roughly four days (2.1 percent of the overall average growing season length). Despite this relatively small effect size, middle latitudes (around 41° N) experienced the greatest number of growing season frost days (GSFDs) in the spring and are expected to continue to experience even more GSFDs as the climate warms [38]. In addition, these four days represent up to 27.5 GDDs (°C), which may be a better indicator of adaptation than average date of spring budburst at specific locations. The later onset of budburst among these middle latitude provenances could be an evolutionary adaptation to increased regional GSFDs. The faster and more synchronous fall senescence of the Indiana and Ohio provenances compared to other seed sources was much more pronounced than the differences in spring budburst. However, the date of peak senescence was clearly intermediate between the northern and southern provenances.

The differential growth responses documented among the six provenances in this study can be attributed to a complex interplay between genetic adaptation to local climates and the immediate environmental conditions of the common garden, which cannot be fully accounted for in this single-site study. Nevertheless, these findings resonate with recent studies that highlight the potential for preexisting mismatches between tree species’ genetic adaptations and rapidly changing climates [6]. The significant mortality rates observed in northern seed sources (Minnesota and Wisconsin) post-thinning could be indicative of the adaptive limitations of these provenances under the warmer climatic conditions of the common garden site, which mirror broader climate warming trends [9]. Northern provenance trees simply did not compete well with their faster growing southern

seed-sourced neighbors. In addition, as the climate continues to warm, local white oak provenances may fail to compete with both native and invasive tree species that are better adapted to the warmer and longer growing season.

Precipitation and temperature data representative of the six provenance origins indicate a consistent climatic gradient, with conditions transitioning from colder and drier in the northern locations to warmer and wetter towards the south. Over the course of the 40-year study, annual precipitation increased on average at all seed source locations (Figure 1B). Likewise, annual minimum temperatures also increased on average at all locations (Figure 1C). USDA plant hardiness zones have shifted northward during this period and now predict 2.8 °C to 5.6 °C warmer mean absolute minimum temperatures at all seed source origins [25]. Future climate projections based on the relatively conservative CCSM4 RCP 4.5 model project another temperature increase of 2.8 °C to 5.6 °C at these locations by 2070 [39]. While warming is expected to continue throughout the 21st century and the seasonal distribution of precipitation will vary, annual precipitation totals are not expected to significantly change in eastern North America over the latter half of the century [40]. Therefore, late 21st century conditions in southern Indiana may be similar to pre-1983 conditions in northern Mississippi. Likewise, growing conditions in southern Indiana over the last 40 years appear to be a reasonable analogue to late century conditions in southern Wisconsin and Minnesota [40].

While the 40-year performance of Minnesota and Wisconsin sourced white oaks in southern Indiana demonstrated the potential unsuitability of existing local genetics in a warmer future climate, the excellent performance of northern Mississippi and southern Illinois trees suggests the suitability of relatively southern genetics for the future southern Indiana climate. By sourcing trees from locations with mean absolute minimum temperatures 5.6 to 11.2 °C warmer [25], white oak plantings will be tolerant of current and likely future conditions. Overall, these findings clearly support proactive forest management actions, highlighting the importance of selecting provenances for reforestation and the expectation that assisted migration will help to ensure future forest ecosystem viability and productivity. Continued research is necessary to delve into the genetic underpinnings of climate adaptability, providing forest managers with the knowledge to bolster white oak forest resilience in a changing world.

5. Conclusions

The results of this study underscore the importance of assisted migration as a strategy for forest management and conservation in the context of climate change. In this study, we have comprehensively analyzed the growth and phenological responses of white oak provenances sourced from a wide range of climatic conditions relative to the common garden planting site in southern Indiana. Our findings reveal significant provenance differences in growth patterns and phenological responses, suggesting that white oak climate adaptation may be less plastic than expected. Rather, climate adaptation appears to be closely tied to genetic adaptation to the local environment prior to anthropogenic climate change. These results are critical for understanding the impact of climate change on forest tree species. For forest managers and tree breeders, this study provides essential insights into selecting and managing white oak provenances. This knowledge is crucial for developing effective reforestation and tree improvement programs that can mitigate the adverse effects of climate change and ensure the sustainability of future white oak forest ecosystems.

Author Contributions: Conceptualization, C.D.N. and M.V.C.; methodology, M.V.C., A.M.T. and C.D.N.; formal analysis, A.M.T.; investigation, A.M.T., P.A.O., M.V.C. and C.D.N.; resources, M.V.C. and C.D.N.; data curation, A.M.T., M.V.C. and C.D.N.; writing—original draft preparation, A.M.T.; writing—review and editing, C.D.N., A.M.T., P.A.O. and M.V.C.; visualization, A.M.T.; supervision, C.D.N. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported in part by an appointment to the United States Forest Service (USFS) Research Participation Program administered by the Oak Ridge Institute for Science and Education (ORISE) through an interagency agreement between the U.S. Department of Energy (DOE) and the U.S. Department of Agriculture (USDA). ORISE is managed by ORAU under DOE contract number DE-SC0014664. All opinions expressed in this paper are the author's and do not necessarily reflect the policies and views of USDA, DOE, or ORAU/ORISE.

Data Availability Statement: The data presented in this study are openly available in Dryad; DOI: <https://doi.org/10.5061/dryad.m37pvmd94>.

Acknowledgments: We thank Carolyn Pike, Jim Warren, Lee Grace, Maeve Draper, and Michael Rich for their help with fieldwork as well as Michael Rich and John Lhotka for their help with dendrochronology measurements. We also thank the Indiana Division of Forestry for providing access to the study planting and historical data related to the project, and the University of Kentucky Wood Utilization Center (Quicksand, KY) for producing the increment core mounting blocks.

Conflicts of Interest: The authors declare no conflicts of interest.

References

- Little, E.L., Jr. *Atlas of United States Trees: Volume 1, Conifers and Important Hardwoods*, 1st ed.; U.S. Department of Agriculture, Forest Service: Washington, DC, USA, 1971; Volume 1.
- Abrams, M.D. Distribution, Historical Development and Ecophysiological Attributes of Oak Species in the Eastern United States. *Ann. Sci. For.* **1996**, *53*, 487–512. [[CrossRef](#)]
- Knapp, B.O.; Pallardy, S.G. Forty-Eight Years of Forest Succession: Tree Species Change across Four Forest Types in Mid-Missouri. *Forests* **2018**, *9*, 633. [[CrossRef](#)]
- Abrams, M.D. Fire and the Development of Oak Forests. *BioScience* **1992**, *42*, 346–353. [[CrossRef](#)]
- Fralish, J.S. The Keystone Role of Oak and Hickory in the Central Hardwood Forest. In Proceedings of the Upland Oak Ecology Symposium: History, Current Conditions, and Sustainability, Fayetteville, AK, USA, 7–10 October 2002; U.S. Department of Agriculture, Forest Service, Southern Research Station: Asheville, NC, USA, 2004; pp. 78–87.
- Cavender-Bares, J. Diversification, Adaptation, and Community Assembly of the American Oaks (*Quercus*), a Model Clade for Integrating Ecology and Evolution. *New Phytol.* **2019**, *221*, 669–692. [[CrossRef](#)] [[PubMed](#)]
- Abrams, M.D. Where Has All the White Oak Gone? *BioScience* **2003**, *53*, 927–939. [[CrossRef](#)]
- Dey, D.C. Sustaining Oak Forests in Eastern North America: Regeneration and Recruitment, the Pillars of Sustainability. *For. Sci.* **2014**, *60*, 926–942. [[CrossRef](#)]
- Dhungel, G.; Rossi, D.; Henderson, J.D.; Abt, R.C.; Sheffield, R.; Baker, J. Critical Market Tipping Points for High-Grade White Oak Inventory Decline in the Central Hardwood Region of the United States. *J. For.* **2023**, *121*, 224–234. [[CrossRef](#)]
- Manos, P.S.; Hipp, A.L. An Updated Infrageneric Classification of the North American Oaks (*Quercus* Subgenus *Quercus*): Review of the Contribution of Phylogenomic Data to Biogeography and Species Diversity. *Forests* **2021**, *12*, 786. [[CrossRef](#)]
- Gombau, J.; Cabanillas, P.; Mena, A.; Pérez-Navarro, J.; Ramos, J.; Torner, A.; Fort, F.; Gómez-Alonso, S.; García-Romero, E.; Canals, J.M.; et al. Comparative Study of Volatile Substances and Ellagitannins Released into Wine by *Quercus pyrenaica*, *Quercus petraea* and *Quercus alba* Barrels. *OENO One* **2022**, *56*, 243–255. [[CrossRef](#)]
- Martínez-Gil, A.; Del Alamo-Sanza, M.; Sánchez-Gómez, R.; Nevares, I. Different Woods in Cooperage for Oenology: A Review. *Beverages* **2018**, *4*, 94. [[CrossRef](#)]
- Dhungel, G.; Ochuodho, T.O.; Lhotka, J.M.; Stringer, J.W.; Poudel, K. Sustainability of White Oak (*Quercus alba*) Timber Supply in Kentucky. *J. For.* **2024**, *122*, 79–90. [[CrossRef](#)]
- DeWald, L.E.; Hackworth, Z.J.; Nelson, C.D. White Oak (*Quercus alba*) Genetics and Tree Improvement Program: Range-Wide Collaborative Effort and Early Results. In Proceedings of the Proceedings of the 36th Southern Forest Tree Improvement Conference, Athens, Greece, 7–9 June 2021.
- White Oak Initiative. Assessment & Conservation Plan. Available online: <https://www.whiteoakinitiative.org/assessment-conservation-plan> (accessed on 14 February 2024).
- Saleh, D.; Chen, J.; Leplé, J.-C.; Leroy, T.; Truffaut, L.; Dencausse, B.; Lalanne, C.; Labadie, K.; Lesur, I.; Bert, D.; et al. Genome-Wide Evolutionary Response of European Oaks during the Anthropocene. *Evol. Lett.* **2022**, *6*, 4–20. [[CrossRef](#)]
- Williams, M.I.; Dumroese, R.K. Preparing for Climate Change: Forestry and Assisted Migration. *J. For.* **2013**, *111*, 287–297. [[CrossRef](#)]
- Poupon, V.; Chakraborty, D.; Stejskal, J.; Konrad, H.; Schueler, S.; Lstibůrek, M. Accelerating Adaptation of Forest Trees to Climate Change Using Individual Tree Response Functions. *Front. Plant Sci.* **2021**, *12*, 758221. [[CrossRef](#)] [[PubMed](#)]
- Gustafson, E.J.; Kern, C.C.; Kabrick, J.M. Can Assisted Tree Migration Today Sustain Forest Ecosystem Goods and Services for the Future? *For. Ecol. Manag.* **2023**, *529*, 120723. [[CrossRef](#)]
- Zhu, K.; Woodall, C.W.; Clark, J.S. Failure to Migrate: Lack of Tree Range Expansion in Response to Climate Change. *Glob. Chang. Biol.* **2012**, *18*, 1042–1052. [[CrossRef](#)]

21. Miller, K.M.; McGill, B.J. Land Use and Life History Limit Migration Capacity of Eastern Tree Species. *Glob. Ecol. Biogeogr.* **2017**, *27*, 57–67. [[CrossRef](#)]
22. McKenney, D.W.; Pedlar, J.H.; Lawrence, K.; Campbell, K.; Hutchinson, M.F. Potential Impacts of Climate Change on the Distribution of North American Trees. *BioScience* **2007**, *57*, 939–948. [[CrossRef](#)]
23. Leites, L.P.; Rehfeldt, G.E.; Robinson, A.P.; Crookston, N.L.; Jaquish, B. Possibilities and Limitations of Using Historic Provenance Tests to Infer Forest Species Growth Responses to Climate Change. *Nat. Resour. Model.* **2012**, *25*, 409–433. [[CrossRef](#)]
24. Soil Survey Staff—Natural Resources Conservation Service—United States Department of Agriculture. Web Soil Survey. Available online: <https://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx> (accessed on 3 February 2024).
25. Hanberry, B.B.; Fraser, J.S. *Current and Future Plant Hardiness Zones for the Conterminous United States*; U.S. Department of Agriculture: Madison, WI, USA, 2023.
26. National Centers for Environmental Information. Climate Data Online. Available online: <https://www.ncdc.noaa.gov/cdo-web/> (accessed on 30 November 2023).
27. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2023.
28. Pinheiro, J.; Bates, D. *R Core Team nlme: Linear and Nonlinear Mixed Effects Models*; R Foundation for Statistical Computing: Vienna, Austria, 2023.
29. Canetti, A.; Braz, E.M.; de Mattos, P.P.; Basso, R.O.; Filho, A.F. A New Approach to Maximize the Wood Production in the Sustainable Management of Amazon Forest. *Ann. For. Sci.* **2021**, *78*, 67. [[CrossRef](#)]
30. Schumacher, F.X. A New Growth Curve and Its Applications to Timber Yield Studies. *J. For.* **1939**, *37*, 819–820.
31. Cole, E.F.; Sheldon, B.C. The Shifting Phenological Landscape: Within- and between-Species Variation in Leaf Emergence in a Mixed-Deciduous Woodland. *Ecol. Evol.* **2017**, *7*, 1135–1147. [[CrossRef](#)] [[PubMed](#)]
32. Fritts, H.C. The Relation of Radial Growth to Maximum and Minimum Temperatures in Three Tree Species. *Ecology* **1959**, *40*, 261–265. [[CrossRef](#)]
33. McMaster, G.S.; Wilhelm, W.W. Growing Degree-Days: One Equation, Two Interpretations. *Agric. For. Meteorol.* **1997**, *87*, 291–300. [[CrossRef](#)]
34. Nordt, B.; Hensen, I.; Bucher, S.F.; Freiberg, M.; Primack, R.B.; Stevens, A.-D.; Bonn, A.; Wirth, C.; Jakubka, D.; Plos, C.; et al. The PhenObs Initiative: A Standardised Protocol for Monitoring Phenological Responses to Climate Change Using Herbaceous Plant Species in Botanical Gardens. *Funct. Ecol.* **2021**, *35*, 821–834. [[CrossRef](#)]
35. Global Modeling and Assimilation Office (GMAO). *MERRA-2: 2d,1-inst1_2d_asm_Nx, Hourly, Instantaneous, Single-Level, Assimilation, Single-Level Diagnostics*; National Aeronautics and Space Administration: Washington, DC, USA, 2015.
36. Lawrimore, J.H.; Ray, R.; Applequist, S.; Korzeniewski, B.; Menne, M.J. *Global Summary of the Month (GSOM), Version 1*; NOAA National Centers for Environmental Information: Jackson County, IN, USA, 2016.
37. Clair, B.S.; Howe, G. Genetic Options for Adapting Forests to Climate Change. *West. For.* **2009**, *54*, 9–11.
38. Liu, Q.; Piao, S.; Janssens, I.A.; Fu, Y.; Peng, S.; Lian, X.; Ciais, P.; Myneni, R.B.; Peñuelas, J.; Wang, T. Extension of the Growing Season Increases Vegetation Exposure to Frost. *Nat. Commun.* **2018**, *9*, 426. [[CrossRef](#)]
39. Matthews, S.N.; Iverson, L.R.; Peters, M.P.; Prasad, A.M. *Assessing Potential Climate Change Pressures across the Conterminous United States: Mapping Plant Hardiness Zones, Heat Zones, Growing Degree Days, and Cumulative Drought Severity throughout This Century*; U.S. Department of Agriculture: Madison, WI, USA, 2018; Volume 9, pp. 1–31. [[CrossRef](#)]
40. USGCRP. *Climate Science Special Report*; U.S. Global Change Research Program: Washington, DC, USA, 2017; pp. 1–470.

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.