

Article

Phenological Differentiation in Sugar Maple Populations and Responses of Bud Break to an Experimental Warming

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Abstract: Species with wide geographical ranges exhibit specific adaptations to local climates, which may result in diverging responses among populations to changing conditions. Climate change has advanced spring phenology worldwide, but questions of whether and how the phenological responses to warming differ among individuals across the natural range of a species remain. We conducted two experiments in January and April 2019, and performed daily observations of the timings of bud break in 1-year-old seedlings of sugar maple (*Acer saccharum* Marshall) from 25 Canadian provenances at two thermal conditions (14/10 and 18/14 °C day/night temperature) in a controlled environment. Overall, bud break started 6 days from the beginning of the experiments and finished after 125 days. The earlier events were observed in seedlings originating from the colder sites. Bud break was delayed by 4.8 days per additional degree Celsius in the mean annual temperature at the origin site. Warming advanced the timing of bud break by 17–27 days in January and by 3–8 days in April. Similar advancements in bud break were observed among provenances under warming conditions, which rejected our hypothesis that sugar maple populations have different phenological responses to warming. Our findings confirm the differentiation in ecotypes for the process of bud break in sugar maple. In cases of homogenous spring warming across the native range of sugar maple, similar advancements in bud phenology can be expected in different populations.

Keywords: *Acer saccharum*; bud burst; climate change; ecotype; growth chamber; phenology; temperature

1. Introduction

An earlier bud break induced by rising spring temperatures has been observed in temperate and boreal ecosystems worldwide during the last decades [1–3]. The timing of growth reactivation is not only an essential driver of carbon, water and energy exchanges [4–6], but a major determinant of plant population dynamics and species ranges [7,8]. However, warming climate may also lengthen the time required for chilling accumulation, leading to delayed leaf unfolding [9–13]. For example, the relationship between spring phenology and spring temperature in European species has significantly decreased

from 1980 to 2013 due to warming-related reductions in chilling [14]. A comprehensive understanding of how spring leaf phenology responds to rising temperature therefore still remains challenging.

The patterns of phenological shifts have wide spatial heterogeneity. According to Hopkin's bioclimatic law, plant spring phenology in North America shifts by 4 days for each degree of latitude northward, and 3.3 days for each 100 m increase in elevation [15]. To some extent, this law matches well with remote sensing observations [16] but shows inconsistent trends for recent decades [17]. For example, a study in the European Alps showed that the elevation-induced phenological shift in 1960 was 34 days 1000 m^{-1} conforming to Hopkins' bioclimatic law, while the phenological shift declined by 35% in 2016 [18]. This was attributed to a spatial divergence between warming and the phenological response to temperature [19].

The phenological response to temperature is critical to determine the growing season length and predict the potential impacts of climate change on forest ecosystems [20]. Experiments and observations have reported substantial differences in phenological response to temperature among species [12,21,22]. Accordingly, the phenological models developed to assess the response of forests to climate change, such as the Sequential Model [23] and UniChill Model [24], must consider each species separately. In addition, species spread over wide geographical regions develop populations with functional traits genetically adapted to the local climate, i.e., ecotypes [25]. Phenological differences between populations have been demonstrated by provenance tests [26,27]. A high component of local adaptation within the same species may require treating individual populations independently to improve the reliability of the predictions of these phenological models. However, the within-species phenological response among populations remains scarcely investigated. Chuine et al. [28] observed the variations in phenological response to temperature among populations of six tree species, but their significance depended on species.

Sugar maple (*Acer saccharum* Marshall) is a model species to assess the phenological variation among populations because of its wide and continuous distribution in eastern North America. Genetic studies have shown that Canadian and US sugar maple exhibit differentiation in local populations [29]. Identified regional ecotypes display variation in tolerance to heat and drought, chilling requirements, timing of leaf flush and growth rate [30]. In a common garden experiment, an earlier bud break of sugar maple was observed in northern populations, which demonstrated different sensitivities to temperature among sugar maple populations [31]. We thus expect that sugar maple populations also exhibit different phenological responses to warming conditions. To test this hypothesis, we conducted two experiments in January and April to investigate the timings of bud break in sugar maple from 25 provenances under two thermal conditions. The aim of the study was to compare the timing of bud break and leaf development among sugar maple populations and quantify their changes under changing chilling and forcing conditions. Moreover, given the great social and economic value of sugar maple, this work is of great importance not only in forest ecology under climate change but also in the related industry and agriculture.

2. Materials and Methods

2.1. Origin of the Provenances and Seedling Production

Seedlings were produced from lots of sugar maple seeds representing seed sources collected from 25 stands growing between the 43rd and 49th parallels, corresponding to the distribution of the species in Eastern Canada (Figure 1 and Table 1). The stands containing the mother trees were located in the deciduous and mixed forest of the northern temperate zone. The climate of the area is continental cold to boreal, with cold winters and cool summers. Climatic data of the sites were assessed using BIOSIM version 11.5 (Natural Resources Canada, Sainte-Foy, QC, Canada), which contained historical and spatially referenced daily weather records and provided geographically adjusted long-term data according to the weather stations located near the stands.

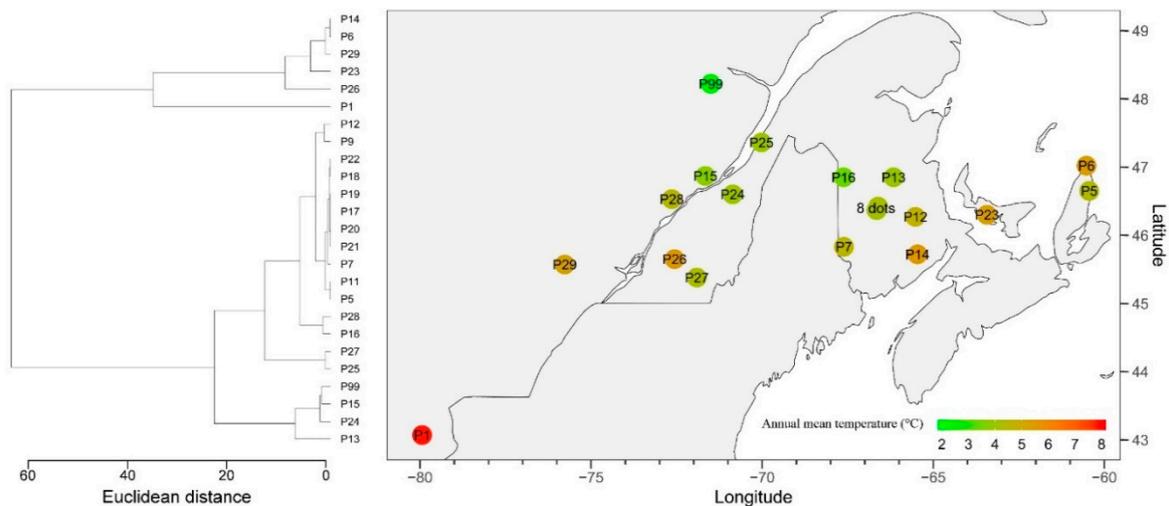


Figure 1. Location, mean annual temperature and frost days of the 25 sites in the study. The point labeled “8 dots” represents P9, P11, P17, P18, P19, P20, P21, and P22. The left panel shows dendrogram generated by a cluster analysis based on the mean annual temperature and number of frost days.

Table 1. Coordinates and climatic characteristics of the sites where seeds were collected, corresponding to the 25 provenances used in the study.

| ID | Latitude (°N) | Longitude (°W) | Annual Temperature (°C) | | | Total Precipitation (mm) | Number of Frost Days |
|-----|---------------|----------------|-------------------------|------|---------|--------------------------|----------------------|
| | | | Minimum | Mean | Maximum | | |
| P1 | 43.07 | 79.95 | 3.25 | 7.93 | 12.68 | 890 | 130 |
| P5 | 46.65 | 60.45 | 0.56 | 4.39 | 8.26 | 1429 | 183 |
| P6 | 47.02 | 60.53 | 1.79 | 5.39 | 9.03 | 1259 | 164 |
| P7 | 45.83 | 67.62 | -1.27 | 4.58 | 10.46 | 1064 | 182 |
| P9 | 46.37 | 66.67 | -1.47 | 4.04 | 9.58 | 1102 | 181 |
| P11 | 46.42 | 66.62 | -1.20 | 4.37 | 10.00 | 1072 | 183 |
| P12 | 46.27 | 65.53 | -0.97 | 4.70 | 10.43 | 1149 | 180 |
| P13 | 46.85 | 66.17 | -1.59 | 3.95 | 9.55 | 1078 | 193 |
| P14 | 45.72 | 65.47 | -0.01 | 5.52 | 11.10 | 1137 | 164 |
| P15 | 46.87 | 71.67 | -1.29 | 3.70 | 8.72 | 1144 | 188 |
| P16 | 46.85 | 67.63 | -2.11 | 3.35 | 8.88 | 1018 | 177 |
| P17 | 46.37 | 66.66 | -1.46 | 4.05 | 9.59 | 1099 | 182 |
| P18 | 46.41 | 66.62 | -1.32 | 4.22 | 9.81 | 1086 | 182 |
| P19 | 46.37 | 66.66 | -1.46 | 4.05 | 9.59 | 1099 | 182 |
| P20 | 46.37 | 66.66 | -1.46 | 4.05 | 9.59 | 1099 | 182 |
| P21 | 46.37 | 66.66 | -1.46 | 4.05 | 9.59 | 1099 | 182 |
| P22 | 46.41 | 66.62 | -1.32 | 4.22 | 9.81 | 1086 | 182 |
| P23 | 46.30 | 63.44 | 1.03 | 5.30 | 9.61 | 1138 | 161 |
| P24 | 46.60 | 70.87 | -0.92 | 4.05 | 9.07 | 1062 | 186 |
| P25 | 47.36 | 70.03 | -0.68 | 4.03 | 8.77 | 954 | 170 |
| P26 | 45.65 | 72.57 | 0.04 | 5.47 | 10.93 | 1017 | 156 |
| P27 | 45.38 | 71.92 | -1.40 | 4.31 | 10.07 | 1094 | 171 |
| P28 | 46.53 | 72.65 | -0.72 | 4.52 | 9.81 | 1048 | 178 |
| P29 | 45.57 | 75.78 | 0.23 | 5.22 | 10.25 | 891 | 165 |
| P99 | 48.22 | 71.51 | -3.16 | 2.25 | 7.66 | 953 | 187 |

In May 2018, the seeds were stratified, and sown in plastic containers with 15 cavities of 320 cm³ volume in the forest nursery of Berthier (QC, Canada). The resulting seedlings were grown in tunnels until the end of June. In July, after two weeks under a shading net, the seedlings were grown in an open space under full light. In November, the seedlings were removed from the containers, and stored in the dark, at a temperature of -2 °C and relative humidity of 85%.

2.2. Experimental Design and Bud Break Assessment

In 2019, we conducted two experiments starting on 27 January and 8 April (experiment 1 and 2, respectively) to assess the effect of chilling accumulation on bud break. Seedlings in experiment 2, with a longer winter by 70 more days, accumulated more chilling than experiment 1. The experiments were performed in two growth chambers Conviron (Winnipeg, MB, Canada). Before each experiment, the seedlings were transferred into a refrigerator at 5 °C for 2 days to acclimate. Each growth chamber involved five containers with 15 cavities. Each container was filled by seedlings from 5 seed sources, with 3 seedlings per seed source for a total of 150 seedlings monitored per experiment. Two thermal treatments were set in each experiment, specifically day/night temperatures of 14/10 °C and 18/14 °C, to assess the effect of forcing on bud break. The temperatures 18 and 14 °C represent the daily range generally observed during bud break in maple stands [32]. During the experiments, photoperiod was maintained at 12 h to attain the same daily heat sum in the thermal treatments, with lighting conditions set at 260–300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. This intensity was chosen to avoid potential warming effects of lights on buds and leaves [25]. Irrigation was supplied daily to maintain soil conditions similar to those occurring in the field during spring.

Seedlings were monitored daily to assess the dates of apical bud break, which were reported as days from the beginning of the experiment. The following five phases of bud break were recorded: (i) bud swell, with slightly reddish scales and enlarging bud; (ii) green tip stage, with the tip and area between the scales light green but no open bud; (iii) bud break, with the loosened scales but barely visible expanding leaf tips; (iv) extended bud break, with leaf bundle expanded beyond the scales but no separated leaves; and (v) full leaf expansion, with flattened and fully expanded leaves [33].

2.3. Statistical Analyses

A cluster analysis using the average linkage method was performed to assess the distance between the location of seed sources based on the mean annual temperature and number of frost days reported in Table 1. The distance between two clusters was the mean Euclidean distance between groups, which were represented by the sites.

One-way analysis of variance was then used to assess the difference in timings of each bud break phase among provenances. Due to the sample size, a bootstrap procedure with 1000 replications was applied to make the results independent from the sample size and improve the reliability of the statistics. Before the analysis, Levene's test was performed to evaluate the homogeneity of variance.

The effect of provenance and thermal treatment on the timings of bud break was evaluated using mixed models, with seedlings being included as a random factor. The mean annual temperature of the origin sites was used to represent the effect of provenance. Data distributions and residuals were checked before and after performing the models, respectively. Multiple comparisons were tested by Welch–Satterthwaite tests. The statistics were applied using *car* v3.0-6, *stats* v3.6.2 and *lmerTest* v3.1-1 package in R (<http://cran.r-project.org>).

3. Results

3.1. Temperature Variation across Sites

The mean annual temperature across the studied sites ranged by more than 5 °C, from 2.3 °C in P99 to 7.9 °C in P1 (Table 1). All sites had a cold winter, with mean daily temperatures < 0 °C for periods varying between 130 and 193 days in P1 and P13, respectively. The sites were grouped in four main clusters based on mean annual temperature and number of frost days (Figure 1). Warmer sites were included in the first cluster, with a mean annual temperature of 5.4 °C and 162 frost days. The second cluster represented the warmest site (P1) of the data set. The third cluster included 15 sites, with mean annual temperatures of ca. 4.2 °C and 170–185 frost days. The sites of the fourth cluster were characterized by the lowest temperature and more than 185 frost days. No geographical pattern was observed in the spatial distribution of the four clusters (Figure 1).

3.2. Timings of Bud Break across Sites

The timings of bud break phases in the two experiments were different among sites, as revealed by the significant *F*-values, ranging from 3.41 to 5.91 ($p < 0.01$) (Table 2). The first phase occurred the earliest in P99, 27.5 and 5.5 days after the beginning of experiments 1 and 2, respectively. P1 was the latest provenance starting bud break, 98 and 19.7 days after the beginning of experiments 1 and 2, respectively. The earliest and latest provenances were the same for all stages of bud break, except for green tip stage in experiment 2 and the stages of bud break and full leaf expansion in experiment 1. The earliest provenance for green tip stage in experiment 2 was P18. In experiment 1, the latest provenances for bud break and full leaf expansion were P7 and P12, respectively.

Table 2. Parameter (*F*-value and *p*) of one-way analysis of variance in the timings of each bud break phase in the two experiments using provenances as factor.

| Experiment | Phase | <i>F</i> -Value | <i>p</i> |
|------------|---------------------|-----------------|----------|
| 1 | Bud swell | 5.06 | <0.001 |
| | Green tip stage | 5.23 | <0.001 |
| | Bud break | 4.71 | <0.001 |
| | Extended bud break | 4.24 | <0.001 |
| | Full leaf expansion | 3.89 | <0.001 |
| 2 | Bud swell | 4.10 | <0.001 |
| | Green tip stage | 5.91 | <0.001 |
| | Bud break | 5.91 | <0.001 |
| | Extended bud break | 5.09 | <0.001 |
| | Full leaf expansion | 3.41 | <0.001 |

3.3. Effects of Provenance and Thermal Treatment

All mixed models were significant ($p < 0.05$) and exhibited a χ^2 ranging from 203.21 to 818.87 (Table 3). Studentized residuals exceeding the 95% confidence interval (the range between -1.96 and 1.96) were 3.4–8.0%, depending on the phenological phase. Residuals showed no trend and were well distributed around zero, suggesting that the models could be considered reliable and representative (Figure S1).

Table 3. Linear mixed model (LMM) comparisons of the timing of each bud break phase (days from the beginning of the experiment) in sugar maple resulting from the two experiments using mean annual temperature at the origin site (TP), thermal treatment in growth chamber (TT), and their interaction as effects, as well as the least-squares mean (LS-mean) when a given phenological phase was observed at day/night temperatures of 14/10 (Colder) and 18/14 °C (Warmer), respectively. Three asterisks indicate $p < 0.001$. LS-Mean values bearing different letters within rows are statistically different at 0.05 probability.

| Experiment | Phase | χ^2 | F-Value | | | LS-Mean | |
|------------|---------------------|----------|-----------|------------|----------------|---------------------|--------------------|
| | | | TP | TT | TP \times TT | Colder | Warmer |
| 1 | Bud swell | 818.87 | 22.04 *** | 26.97 *** | 0.15 | 79.01 ^a | 61.53 ^b |
| | Green tip stage | 636.60 | 33.12 *** | 56.68 *** | 0.12 | 89.02 ^a | 66.30 ^b |
| | Bud break | 572.82 | 21.16 *** | 38.52 *** | 1.14 | 92.36 ^a | 72.38 ^b |
| | Extended bud break | 647.34 | 23.62 *** | 66.95 *** | 1.42 | 96.79 ^a | 74.77 ^b |
| | Full leaf expansion | 680.33 | 17.54 *** | 101.35 *** | 0.76 | 106.55 ^a | 79.48 ^b |
| 2 | Bud swell | 266.17 | 24.41 *** | 25.70 *** | 0.20 | 11.06 ^a | 7.58 ^b |
| | Green tip stage | 203.21 | 51.29 *** | 60.75 *** | 0.00 | 16.03 ^a | 10.74 ^b |
| | Bud break | 234.42 | 74.39 *** | 64.42 *** | 1.42 | 18.99 ^a | 12.97 ^b |
| | Extended bud break | 259.30 | 68.75 *** | 110.45 *** | 0.07 | 21.54 ^a | 14.93 ^b |
| | Full leaf expansion | 248.35 | 58.46 *** | 167.32 *** | 2.13 | 30.31 ^a | 21.58 ^b |

The provenance, represented in the models by the mean annual temperature of the provenance origin, affected bud break ($p < 0.001$) (Table 3). The provenances belonging to warmer sites had later bud breaks (Figure 2). Overall, bud break was delayed by 4.76 days per additional degree Celsius of mean annual temperature of the origin site.

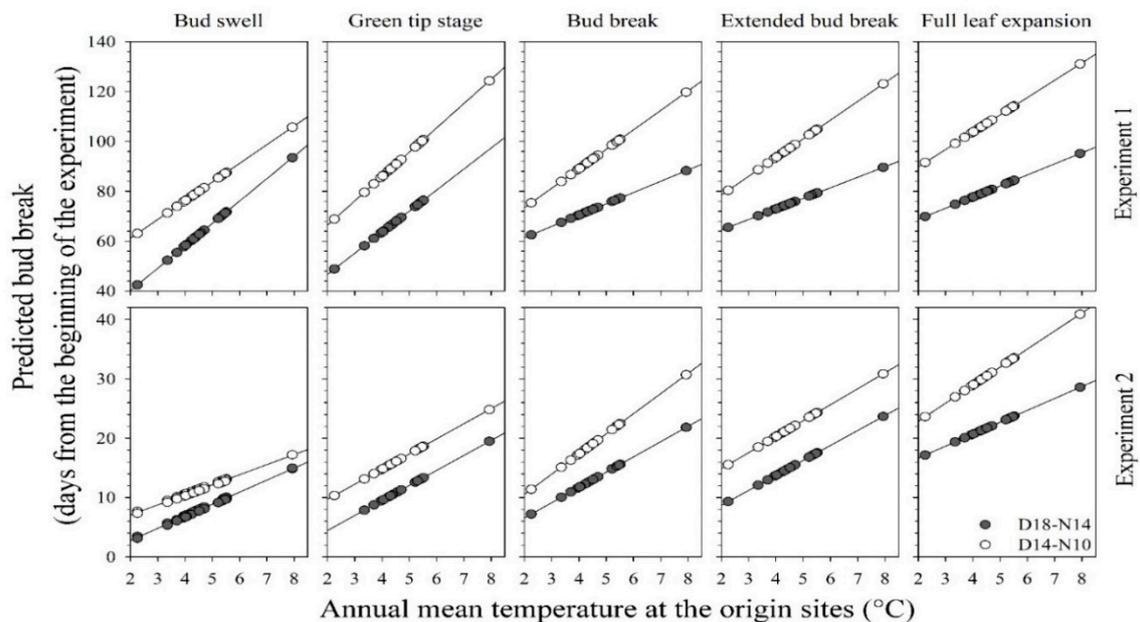


Figure 2. Days of occurrence of the five phases of bud break predicted for sugar maple by the linear mixed model (LMM) performed on data of the two experiments at control and warming treatments. Dots represent the different provenances. White and grey dots refer to day/night temperatures of 14/10 and 18/14 °C, respectively. The ranges of y -axis are different.

Thermal treatment had a significant effect on the timings of bud break, as F -value ranged from 25.70 to 167.32 ($p < 0.001$) (Table 3). Higher temperature significantly advanced the timing of bud break phases. In experiment 1, seedlings submitted to warmer temperature exhibited an advancement of 17.48 to 27.07 days depending on the bud break phases. In experiment 2, this advancement was 3.48 days in the first phase, and increased to 8.71 days in the last phase. No provenance \times thermal treatment interaction was observed, indicating that the thermal treatment produced the same effect irrespective of provenance of the seedlings (Table 3).

4. Discussion

This study described the timings of bud break in sugar maple populations and assessed their responses to a simulated warming under controlled conditions. We observed a linear relationship between timing of bud break and temperature of the provenance origin. Our experiments demonstrated that higher temperature can advance the timings of bud break, but the effects were similar among provenances. This finding is novel for sugar maple and contradicted our hypothesis that sugar maple populations have different phenological responses to warming.

4.1. Timings of Bud Break Differ among Provenances

Mean annual temperatures decrease towards the pole, with a rate of 0.73 °C per degree of latitude in the Northern extratropical hemisphere [34]. A strong pattern of bud phenology in sugar maple along a latitudinal gradient could thus be expected, which was in accordance with the common garden experiment of Kriebel [31], showing that leaf-out of sugar maple occurs earlier in northern than southern provenances. However, there was no latitudinal trend of the temperature variation among provenances in this study, which was related to the maritime-continental effects. The heating capacity of water is higher than that of land, leading to lower annual temperature variation close to the sea, thus disrupting the expected thermal pattern along a latitudinal gradient.

This variation in the timing of bud break among provenances confirmed the presence of ecotypes, i.e., the differentiation in local populations of sugar maple, and reflected the spatial

diversity in chilling and forcing needs. As shown by a previous garden experiment of sugar maple, northern provenances, which usually correspond to colder provenances, required more chilling for endodormancy release but less forcing for triggering bud break than southern provenances [35]. Similarly, a recent study using bud break models also showed that the chilling requirement of white ash increased by 3.1 daily chilling units per degree of latitude and the forcing requirement decreased by 14.1 degree days per degree of latitude [36]. In northern regions, or at colder provenances, optimal timing of bud break was in late spring, when frost events are unlikely to occur. The difference in requirements seems to be the result of an evolutionary trade-off between survival (mainly avoidance of frost damage) and growth.

4.2. Converging Responses of Populations to Temperature

Our results showed that the responses of bud break to rising temperature were similar among sugar maple provenances. Along altitudinal and temporal gradients, Vitasse et al. [20] reported different populations of the same species exhibited an advancement of about 2.1, 6.7 and 7.4 days, $8\text{ }^{\circ}\text{C}^{-1}$, for European beech (*Fagus sylvatica* L.), common ash (*Fraxinus excelsior* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.), respectively, suggesting that the phenological responses to temperature are constant within broadleaf species, despite the presence of local adaptation. Similar results were also found in conifers, such as the boreal black spruce (*Picea mariana* (Mill.) BSP) [25]. Chuine et al. [28] detected no difference in the phenological responses to temperature between populations in common hornbeam (*Carpinus betulus* L.), common alder (*Alnus glutinosa* Gaertn.) and smooth-leaved elm (*Ulmus minor* Mill.). Thus, similar advancements of bud break can be expected in the different provenances, in the case of spring warming arriving at the same rate across the species range.

Our finding suggests that phenological model parameters set for specific populations could be applied reliably to other populations of the same species [28]. However, the future spatial pattern in phenology also depends on the warming pattern and heterogeneity across the species distribution [18,19]. As a result, the faster spring warming expected at higher latitudes [37] will probably make the prediction of the timings of bud break among provenances more complex than anticipated.

5. Conclusions

Understanding and predicting the impacts of a changing climate on terrestrial ecosystems requires investigations of how plant phenology advance under warming, and whether populations of the same species respond to these changes. In this study, we monitored daily the timings of bud break in sugar maple from 25 Canadian provenances under two thermal conditions to verify whether and how the phenological responses to temperature differ among populations. Our results showed that the timings of bud break differed among populations and were negatively correlated with the mean annual temperature at the provenance origin. The provenance \times thermal treatment interaction was not significant, which rejected the hypothesis that sugar maple populations have different phenological responses to warming. We conclude that similar advancements of bud break could be expected in this species under a scenario of homogeneous warming across the Canadian range of sugar maple. Our results suggest that the parameters of phenological models set for specific populations could be applied reliably to other populations of the same species. However, the spatial differences in warming expected under the ongoing climate change could make the predictions of bud break in wide geographical areas more complex than expected.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/11/9/929/s1>, Figure S1: Studentized residuals vs predicted values resulting from the mixed models performed on the timing of bud break in sugar maple. The range between -1.96 and 1.96 indicates the 95% confidence interval.

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

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