

Phenological Plasticity and Adaptive Potential of Sugar Maple Populations

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Abstract

Global changes affect the growing conditions of terrestrial ecosystems, mismatching the phenological adaptation of plants to local climates at mid and high latitudes. Their long lifespan and slow reproductive cycles prevent trees from tracking the quick shift in their usual climatic conditions, thus endangering the survival of local populations. In this study, we explored the phenological plasticity and adaptive potential of bud burst in sugar maple (*Acer saccharum* Marsh.) seedlings from 30 Canadian origins with contrasting climates planted in two common gardens near and at the northern boundary of the species range. Bud development and leafing occurred in April-May, with complete bud burst lasting between 21 and 29 days. On average, bud swelling differed by 12 days between common gardens. However, this difference decreased to 4 days for complete leafing. Both factors site and seed origin affected bud burst, which represented the phenological plasticity and adaptation of sugar maple, respectively. Overall, the former (7.4–88.3%) contributed more than the latter (9.2–25.5%) to the variance in bud burst, despite the wide climatic range among the provenance origins compared with that at the two common gardens. Adaptation to local conditions provide the genetic tools for the survival of species across wide climatic ranges. Plasticity enables physiological responses of individuals to quick environmental changes. Our study demonstrated the major role of plasticity in bud phenology, and revealed the importance of investing resources in mechanisms dealing with the climatic challenges due to inter-annual variations in weather events.

Introduction

Climate change is altering the growing conditions of plants in terrestrial ecosystems, and mainly tree growth at mid and high latitudes. In order to survive under such a rapid change, plants can either track their usual conditions through migration (Angert et al. 2011; Chen et al., 2011), or change their growth strategies to match the novel climate *in situ* (Aitken et al. 2008; Hoffmann and Sgrò 2011). However, given their long lifespan, slow regeneration cycles, the presence of geographical barriers (Scheller and Mladenoff 2008), and the rapid rates of climate change (Gray and Hamann 2013), trees could be unable to match the new environmental conditions. Under such a context, the ability to deal locally with a changing climate could be a critical factor for the survival of local populations in the medium and long term.

Phenology describes the recurring sequence of biological events during the plant cycle, such as bud burst, flowering, and leaf senescence (Richardson et al. 2013). Among this sequence, the timings of bud burst in spring and the beginning of the growing season have received a lot attention given the close relationship with carbon sequestration and growth. An earlier bud burst is related to a longer growing season (Leinonen and Kramer 2002), allowing plants to produce more carbohydrates to invest in growth and reserves. The accumulation of cold temperatures in autumn and winter (chilling), heat in spring (forcing), and hours of light (photoperiod) are the important factors involved in growth reactivation (Arora et al. 2003; Chen et al. 2019; Huang et al. 2020) and can affect the annual time window when trees can perform photosynthesis. Previous studies have demonstrated that climate warming has strongly

advanced bud phenology due to the earlier fulfilment of forcing, resulting in an increased carbon sequestration in trees (Bronson et al. 2009). However, the question of the adaptive potential of phenology to climate variations remains unanswered.

Local adaptation is a long-term evolutionary process driven by natural selection. In a given site, the genotypes better matching local growing conditions survive and are maintained within the population. Thus, local genotypes show a higher fitness in their home environment (Kawecki and Ebert 2004). Numerous studies have shown the local adaptation regarding a number of functional traits, such as plant diameter (Gárate-Escamilla et al. 2019), height (Beaulieu et al. 2004), leaf area (Roybal and Butterfield 2018), and bud phenology (Salmela et al. 2013; Silvestro et al. 2019). For example, in a cold environment, where the growing season is limited by low temperatures, trees tend to have a lower forcing requirement, allowing bud burst to start earlier to take advantage of the favorable growing conditions (Guo et al. 2020).

Phenotypic plasticity is the ability of a genotype to express different phenotypes within a range of environmental conditions (Nicotra et al. 2010). Plants invest resources in the synthesis of special compounds for maintenance costs, which allows information to be obtained on the surrounding conditions (Auld et al. 2010). Once the signals of environmental change are detected, alternative reaction norms, a series of phenotypes, could be induced to cope with the new conditions. These multiple phenotypes have different fitness, some of them inevitably mismatching the environmental conditions, with consequent maladaptation (Ghalambor et al. 2007). As an important component of fitness, phenotypic plasticity enables species to respond quickly, and more quicker/faster than genotypic adaptation, to the environment changes (Chevin et al. 2013; Franks et al. 2014). However, high phenotypic plasticity is expensive in terms of maintenance costs, developmental instability (Van Buskirk and Steiner 2009), and the potential occurrence of maladaptation.

Local adaptation and plasticity are two important strategies for plants to deal with climate change. However, no consensus has been reached on the relative importance of them. For example, some studies demonstrated a dominant role of local adaptation in mediating the relationship between functional traits and environment (Leimu & Fischer 2008; Laughlin & Messier 2015). Others have shown that plasticity exceeds adaptation in explaining the variation of tree height (Gárate-Escamilla et al. 2019), leaf area (Bresson et al. 2011), and bud phenology (Vitasse et al. 2013). A precise estimation of the relative contribution of local adaptation and plasticity can quantify the ability of species to perform across wide distribution ranges, and predict the potential changes of this range under global warming.

Due to its wide distribution range, strong sensitivity to climate, and the economic importance for eastern North America, sugar maple (*Acer saccharum* Marsh.) has been regarded as a model to study the response of species to climate change (Li et al. 2018; Putnam and Reich 2017). Previous studies showed evidence of ecotypic differentiation of bud phenology, mainly regarding the minimum temperatures occurring in spring at the seed origin (Guo et al. 2020; Ren et al. 2020). In this study, we explored the adaptive potential and plasticity of sugar maple on seedlings from 30 Canadian origins planted in two

common gardens near and at the northern boundary of the species range. We aimed to quantify the relative contribution of adaptation and phenotypic plasticity to the variance in bud phenology. We tested the hypothesis that phenotypic plasticity is more important than local adaptation in regulating bud phenology due to the high variability in short-term weather events experienced in this area of the North American continent.

Materials And Methods

Seed origin

A total of 30 stands of sugar maple located across the natural range in Canada were used in this study (Fig. 1). Seeds collected from different stands represent different seed origins. This area is included in the bioclimatic domains of deciduous and mixed forests of the northern temperate zone, which is dominated by both broadleaves and conifers, mainly sugar maple, red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britt) and fir (*Abies balsamea* (L.) Mill.). The climate is continental, with cold winters and warm summers.

Plant material and common garden

The seeds were collected either from single mother trees (National Tree Seed Centre, Natural Resources Canada), or at stand level (Ministère des Forêts, de la Faune et des Parcs) (Table S1). Some seed origins were collected from the same area (Mavis Mills). In 2018, the seeds were used to grow seedlings that were planted in two common gardens located in Chicoutimi and Ripon (QC, Canada) in spring 2019 at a distance of 3 m × 3.5 m. Between 6 and 10 seedlings per origin were planted and submitted to phenological observations, for a total of 217 and 242 seedlings in Chicoutimi and Ripon, respectively.

Phenological observations

We monitored leaf phenology of seedlings twice per week in 2020. Eight phases of bud and leaf development were recorded according to Skinner and Parker (1994): (1) bud swell, with reddish scales and enlarging bud; (2) bud elongation, with a yellowish color between the scales; (3) green tip stage, with the tip and area between the scales light green but closed bud; (4) bud break, with loosened scales but barely visible expanding leaf tips; (5) extended bud break, with leaf bundle expanded beyond the scales but no separated leaves; (6) initial leaf emergence, with the leaves starting to expand perpendicularly to the base of the bud; (7) initial leaf expansion, with light green, small, and wrinkled leaves; and (8) full leaf expansion, with flattened and fully expanded leaves.

Climate data extraction and bioclimatic index computation

Minimum, maximum, mean temperature and precipitation during 1979–2020 were extracted according to the coordinates of all seed origins and common gardens, from ERA5 dataset on Google Earth Engine (Copernicus Climate Change Service 2017; Gorelick et al. 2017). The 19 bioclimatic variables proposed by

O'Donnell and Ignizio (2012) were extracted with the *biovars* function of the *dismo* package (Hijmans et al. 2020).

Statistical analyses

A Principal Component Analysis (PCA) was performed based on the 19 bioclimatic variables to describe the annual trend, seasonality and extreme conditions across seed origins and between common gardens. The contribution of each bioclimatic variable to the total variance explained by the principal components was determined. We applied a generalized linear model to test the effects of phase, site (common garden), and their interaction on bud phenology of sugar maple. The effects of provenance and individuals were set as random factors. We tested the effect of plasticity (i.e. the factor site) and adaptation (i.e. the factor seed origin) on variance partitioning for the different phenological phases using the non-parametric procedure PERmutational Multivariate Analysis Of Variance (PERMANOVA) (Anderson et al. 2011) based on the *adonis* function, with metric Euclidean distance matrix (McArdle and Anderson 2001) and 10000 permutations. The relative contribution of site, seed origin, and their interaction to the variance of bud phenology were further calculated using PERMANOVA. All the statistics were performed in R (R Core Team 2020) using the *MuMin* and *vegan* packages (Oksanen et al. 2020).

Results

Climate and bioclimate of the study sites

The mean annual temperature of the seed origins ranged between 2.6 and 8.4°C, recorded at seed origin 30 and 1, respectively (Table S1). On average of all seed origins, minimum and maximum mean annual temperature was -7.9 and 18.3°C, respectively. With a minimum mean annual temperature of -11.1°C, and a maximum mean annual temperature of 16.6°C, seed origin 30 was the coldest site. Seed origin 1 was the warmest site, showing a minimum mean annual temperature of -4.8°C, and a maximum of 21.9°C (Table S1). The mean annual temperature in Ripon was 4.5°C, warmer than that in Chicoutimi (3.2°C). Annual precipitation ranged between 947 and 4924 mm, increasing towards east.

PCA extracted three main principal components (PC), explaining 44.4, 26.3, and 21.2% of the variability in the bioclimatic variables for seed origins and common gardens (Table S2). PC1 separated continental and oceanic climates, situated on the left and right quadrants, respectively (Fig. 2). Thus, the seed origins located inland had a more continental climate (higher temperature variability at seasonal and yearly scale represented by bio 4 and bio 7) than those close to the Gulf of Saint Lawrence River (Fig. 1). PC2 separated locations characterized by different precipitation regimes. The seed origins located in the westernmost part were generally drier (lower precipitation during the wettest period, represented by bio 16 and bio 13) than those close to the Saint Lawrence River. PC3 separated seed origins by the isothermality, i.e. the ratio between mean diurnal range and temperature annual range. Seed origins located inland showed a higher isothermality (bio 3) than those close to the Gulf of Saint Lawrence River (Fig. 2).

Ripon and Chicoutimi, the two common gardens, were located in the upper quadrant on the right side of PCA (Fig. 2). Compared with most seed origins, they were characterized by colder winter temperatures (bio 6 and bio 9) and higher seasonality and annual range in temperature (bio 4 and bio 7). Chicoutimi had a higher temperature seasonality (bio 4) than Ripon.

Bud and leaf phenology

Bud and leaf phenology occurred earlier in Ripon than Chicoutimi (Fig. 3). On average, phase 1 started on DOY 121 in Ripon, 12 days earlier than Chicoutimi (DOY 133). The difference in bud phenology between the two sites decreased with the successive phases. Seedlings in Ripon exhibited phase 8 on DOY 150, only 4 days earlier than Chicoutimi (DOY 154). Overall, the period of leafing lasted 29 and 21 days in Ripon and Chicoutimi, respectively. The generalized linear model demonstrated the differences observed, calculating significant effects of phase ($F = 5691.4, p < 0.0001$), site ($F = 523.2, p < 0.0001$), and their interaction ($F = 253.2, p < 0.0001$) in determining the timing of bud burst. The marginal R^2 and conditional R^2 of the generalized linear model were 0.93 and 0.95, respectively, demonstrating the high fitness of the model.

Variance components

PERMANOVA confirmed the effect of site for all phases of leaf development ($p < 0.001$), with Ripon showing the earliest growth reactivation. The effect of seed origin was significant at the beginning (phases 1–3) and ending (phases 7–8) of leaf development ($p < 0.05$, Table 2). The effect of seed origin indicated that populations had different timings of bud and leaf development. The interaction site \times seed origin was significant for phases 2, 7 and 8 ($p < 0.05$), suggesting that the difference of bud phenology between the two common gardens changed according to the seed origin.

The factor site explained most variance in leaf development, between 7.4 and 88.3% (Fig. 4). The importance of the site was highest at the beginning, decreasing with the successive phenological phases. Overall, seed origin and site \times seed origin contributed with a lower proportion of the variance, between 11.7 and 26.7%. For all phases, the variance component of seed origin (9.2–25.5%) was higher than the interaction site \times seed origin (1.1–9.3%). Both variance components of seed origin and site \times seed origin increased from phase 1 to phase 7. The residuals accounted for an increasing variance in bud phenology, from 11.1% for phase 1 to 58% for phase 8.

Discussion

4.1 Plasticity of bud phenology

The significant effect of site on bud phenology indicated a significant phenotypic plasticity of leaf development for sugar maple. As sessile organisms, plants benefit from a high phenological plasticity to respond quickly to environmental changes, matching the optimal moment of the year for flushing, and avoiding the negative consequences of early or late growth reactivations (Allevato et al. 2019).

Individuals with high phenological plasticity in bud phenology are favored during the evolutionary process (Vitasse et al. 2010). This phenological plasticity of sugar maple may be an important factor that enables a broad tolerance of the species to various environmental conditions, and probably contributes to the wide latitudinal range of the species across eastern North America.

The interaction between site and seed origin at the beginning and ending of leaf development indicated differences in phenological plasticity among sugar maple populations. These different responses may be related to contrasting adaptation strategies among populations within the same species, and involving the trade-off between lengthening the growing season and avoiding frost damages. In six temperate deciduous species, the phenological plasticity was lower in populations originating from higher elevations (Vitasse et al. 2013). A lower plasticity limits the sensitivity to warmer spring temperatures, thus delaying bud burst and ensuring the avoidance of frost. A high plasticity is expensive for plants, and requires resources for the continuous monitoring of the environment through the synthesis or use of chemical substances (Van Buskirk and Steiner 2009). For *Pinus contorta* and *Pinus monticola* growing under stressing conditions, more resources were invested to resist drought and frost, thus, a reduced plasticity was observed for growth (Chuine et al. 2006). This different magnitude of plasticity among populations plays an important role in matching environmental changes and ensuring sustained growth in the long term.

4.2 Comparison of bud phenology in two common gardens

Buds of sugar maple reactivated earlier in the southern plantation (Ripon). In our study, the mean spring temperature (April-May) in 2020 in Ripon was 4.6 °C, which was higher than that in Chicoutimi (2.4 °C). Warmer spring conditions in Ripon speed up the achievement of forcing temperatures, thus advancing bud burst. Our results are consistent with previous studies conducted in temperate and boreal ecosystems. The timings of leaf unfolding of *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. advanced at a rate of 5.7 days per additional degree Celsius along five common gardens (Vitasse et al. 2010). Similarly, buds of *Populus fremontii* in Arizona flush earlier in trees growing in the common gardens of warmer regions (Cooper et al. 2019).

According to the 19 bioclimatic variables, the climatic distance between the two common gardens could be considered small when compared to the broad geographical gradient of the seed origins used in this study. However, we detected a difference of 12 days for the beginning of leaf development between Ripon and Chicoutimi. The two common gardens are located near or at the border of the northern distribution of sugar maple. Individuals growing at the boundary of species distribution are more sensitive to the environment (Jump et al. 2006; Normand et al. 2009). For example, the effects of winter temperature on the radial growth of European beech (*Fagus sylvatica* L.) were significant only at the colder part of the distribution (Weigel et al. 2018). Similarly, European beech was more sensitive to drought at the drier boundary of the range (Jump et al. 2006; Roibu et al. 2017). In our study, the difference in spring

temperature between the two common gardens reached 2.2 °C, which explained the observed delay of bud phenology in Chicoutimi.

The time gap between Ripon and Chicoutimi decreased for the later leafing stages (7 and 8). The difference in photoperiod is an important factor for spring phenology. Day length during bud burst (phase 1) was 15.0 h in Chicoutimi, which was longer than that recorded in Ripon (14.1 h) due to the different latitudes and timings of growth reactivation between common gardens. A longer photoperiod could have speeded up bud development, thus resulting in similar timings of full leaf expansion. A previous study demonstrated that sugar maple leafing benefits from a longer day length, and photoperiod can outweigh the delaying effects of colder springs (Ren et al. 2020). However, the similar ending of leaf expansion in the two common gardens remains partially unexplained, and could result from the weather events occurring during the studied year. Thus, a better understanding of the impact of current weather on leaf development is needed and requires a long-term monitoring of bud phenology in the two common gardens.

4.3 Plasticity vs local adaptation

Our study revealed a higher contribution of plasticity to variance compared with local adaptation, mainly at the beginning of leaf development. Similar results were also observed in other species of boreal and temperate ecosystems (Baliuckas and Pliura 2003; Vitasse et al. 2010). The contribution of plasticity to bud burst phenology ranged from 55 to 86% in seven deciduous species in Europe, one order of magnitude higher than that of local adaptation (0.3-9%) (Vitasse et al. 2013). In another study combining experiments in situ and common garden, the genetic differentiation explained <28% of variance in the morphological and physiological traits of leaves of sessile oak and European beech, suggesting a minor effect of local adaptation on leaf functional traits (Bresson et al. 2011).

Local adaptation and phenotypic plasticity act as concurring processes in the response of plants to changes in the environment, playing a different role at spatial and temporal scales. Under stable local environments, well adapted populations could maintain competitive fitness to survive. However, in a context of rapidly changing conditions, which requires fast response mechanisms (Van Kleunen and Fischer 2005), phenotypic plasticity can be favoured. Species with wide distributions, especially under continental climates, can experience a wide inter-annual variability in environmental conditions, principally temperature, one of the main limiting factors for bud phenology in spring. Individuals with high plasticity can respond to weather events quickly and gain a comparably longer period for carbon fixation and high competitive abilities (Kramer 1995). In addition, because of the long lifespan and slow and intermittent regeneration periods (masting years) of trees, individuals could rely predominantly on phenotypic plasticity for survival and growth rather than adaptation (Fox et al. 2019).

It has been predicted that the mid-latitudes of North America will have experienced warming up to 7 °C at the end of the 21st century (Feng et al. 2014). On the one hand, plastic species may benefit from these changes by lengthening the growing season and increasing fitness. A previous study demonstrated that

the recent advancement of 13 flowering days under global warming has helped plastic trees to improve their fitness by 40% (Anderson et al. 2012). On the other hand, an earlier bud burst seriously increases the risk of frost damage to the young developing tissues and leaves (Howe et al. 2003). Under the ongoing global changes, the climatic variability increases in magnitude, resulting in more frequent extreme weather events such as heat waves (Hegerl et al. 2011; Min et al. 2011) or cooling (Wang et al. 2011). These extreme events have proved to be detrimental for tree growth and survival in the short term. Phenotypic plasticity is an important functional trait to deal with the increased uncertainty of climate in the future (Harmon et al. 2009; Donohue et al. 2013).

In this study, we observed a high contribution of residuals to the variance in bud phenology, which is in agreement with previous studies (Sole-Medina et al. 2020; Varsamis et al. 2018). This large heterogeneity in phenology unexplained by our factors may suggest a high variability among individuals (Perrin et al. 2017), in addition to the potential effect of microsite conditions and sampling errors during field observations. An important effect of microsite on plant phenology seems unlikely, because the two common gardens are located in cropland areas, which were submitted to crop production in the past, and are therefore expected to be more homogeneous than natural sites. The wide variation in bud phenology within the same population may represent a diverse gene reservoir for the long-term survival of the species (Rousi and Heinonen 2007). These various genotypes ensure a potential matching between some individuals of the populations and the environmental conditions, thus allowing local persistence of the species.

Conclusion

Local adaptation and phenotypic plasticity act as concurring processes in the response of plants to environment, whose changes are critical for the survival of local populations. In this study, we explored the adaptive potential and phenological plasticity of sugar maple seedlings from 30 Canadian origins planted in two common gardens near and at the northern boundary of the species range. Plasticity explained up to 88.3% of the total variance for bud burst, while the variance component of adaptation ranged between 9.2 and 25.5%. Sugar maple is distributed over a wide geographical area, at different latitudes and distances from the sea. Under such diverging conditions, this species deals with complex climatic dynamics, involving different patterns of growing season length and frost risk (Guo et al. 2020). Adaptive mechanisms allow phenology to better match with local climates, thus ensuring a tolerance to wide environmental conditions. On the other hand, weather events are partially unstable, and populations face such a changing environment throughout their lifespan. In this context, the plasticity allows individuals to respond quickly to environmental changes, despite the high costs in resources required to maintain plasticity. Our study assessed the importance of plasticity and adaptation and interpreted their role under different temporal and spatial scales, respectively. Phenology could benefit from the high plasticity observed in sugar maple to cope with the challenge that climate warming will impose for the survival of local populations.

Declarations

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Conflict of Interest

The authors declare that they have no conflict of interest

Ethics approval (include appropriate approvals or waivers)

'Not applicable'

Consent to participate (include appropriate statements)

All patients included in this study gave written informed consent to participate in this research.

Consent for publication (include appropriate statements)

All patients included in this research gave written informed consent to publish the data and images contained within this case report.

Availability of data and material (data transparency)

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability (software application or custom code)

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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Table

Table 1

Effect of site, seed origin and their interaction on bud and leaf phenology in sugar maple seedlings. One, two, and three asterisks indicate $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively

	Site	Seed origin	Site×seed origin
Phase 1	1581.67***	2.84***	1.24
Phase 2	1255.77***	3.01***	0.01**
Phase 3	1051.76***	3.04***	0.61
Phase 4	337.88***	1.44	0.74
Phase 5	139.51***	1.15	0.65
Phase 6	37.94***	1.23	0.86
Phase 7	52.07***	2.46***	1.69*
Phase 8	159.85***	1.74*	2.53***

Figures

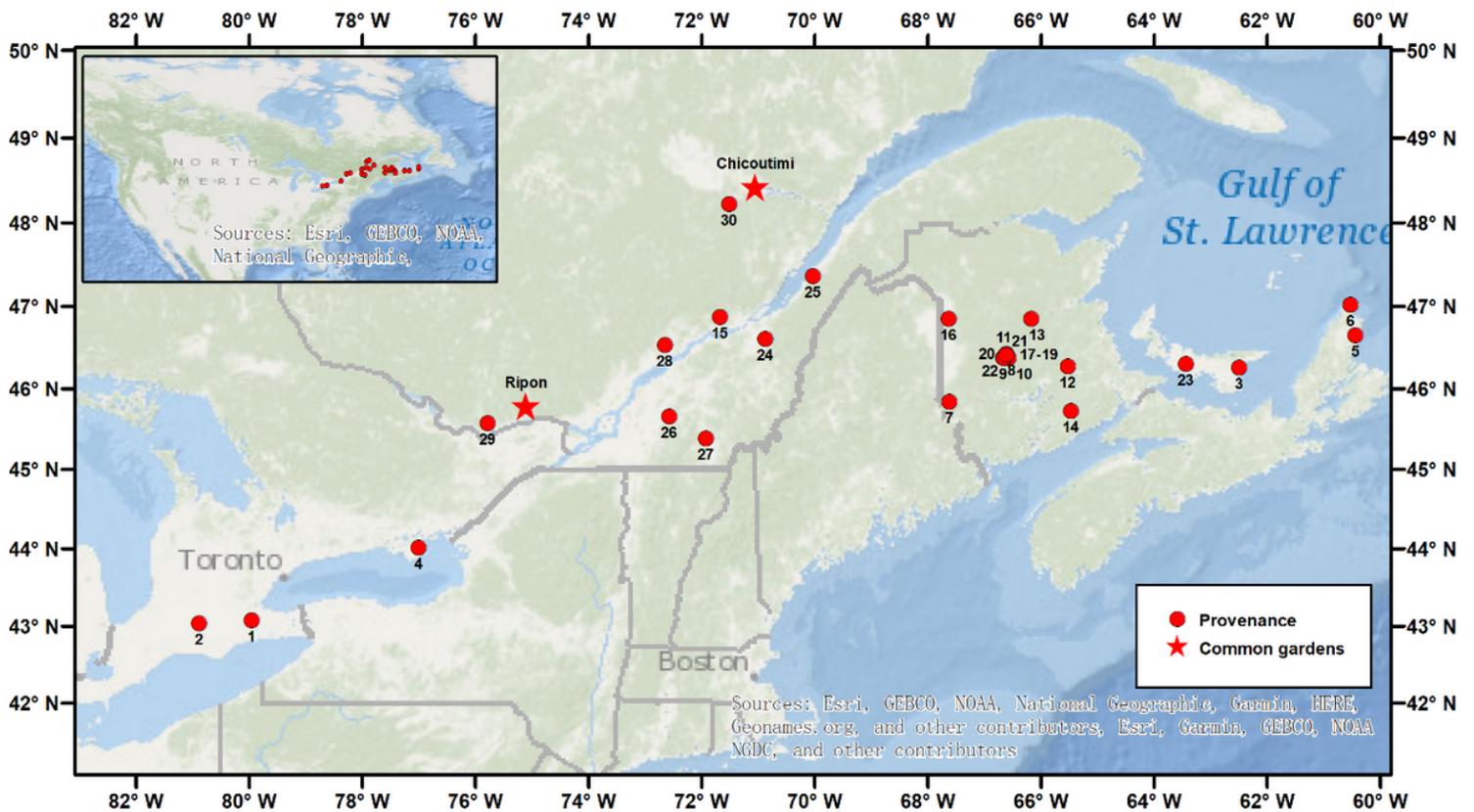


Figure 1

Location of the 30 seed origins of sugar maple. The stars mark the location of the two common gardens in Chicoutimi and Ripon.

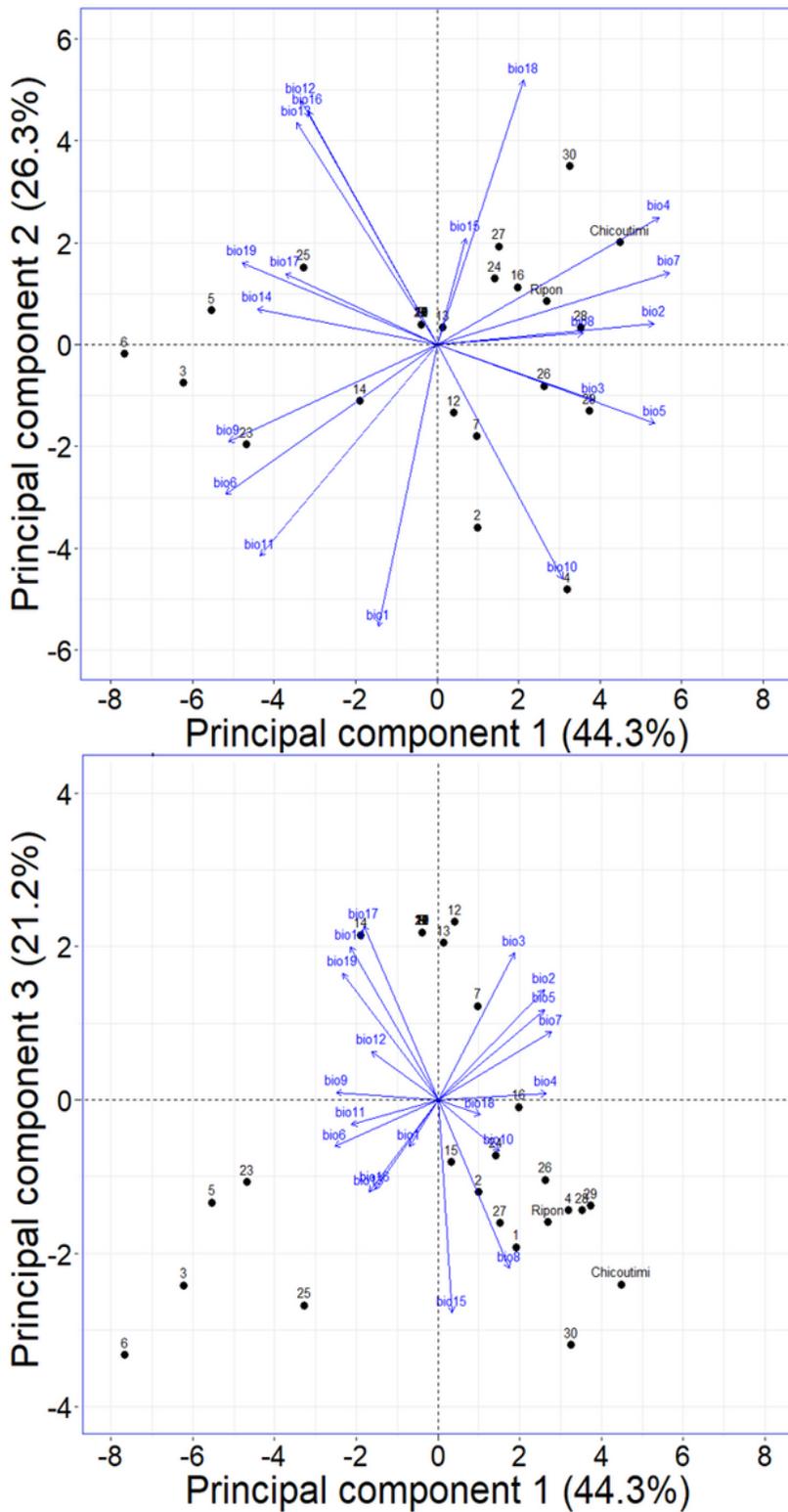


Figure 2

Principal component analysis of the climatic variability between seed origins and common gardens. Bio1: annual mean temperature; bio 2: mean diurnal range; bio3: isothermality; bio4: temperature seasonality; bio5: max temperature of warmest month; bio6: min temperature of coldest month; bio7: temperature annual range; bio8: mean temperature of wettest quarter; bio9: mean temperature of driest quarter; bio10: mean temperature of warmest quarter; bio11: mean temperature of coldest quarter; bio12: annual

precipitation; bio13: precipitation of wettest month; bio14: precipitation of driest month; bio15: precipitation seasonality; bio16: precipitation of wettest quarter; bio17: precipitation of driest quarter; bio18: precipitation of warmest quarter; bio19: precipitation of coldest quarter.

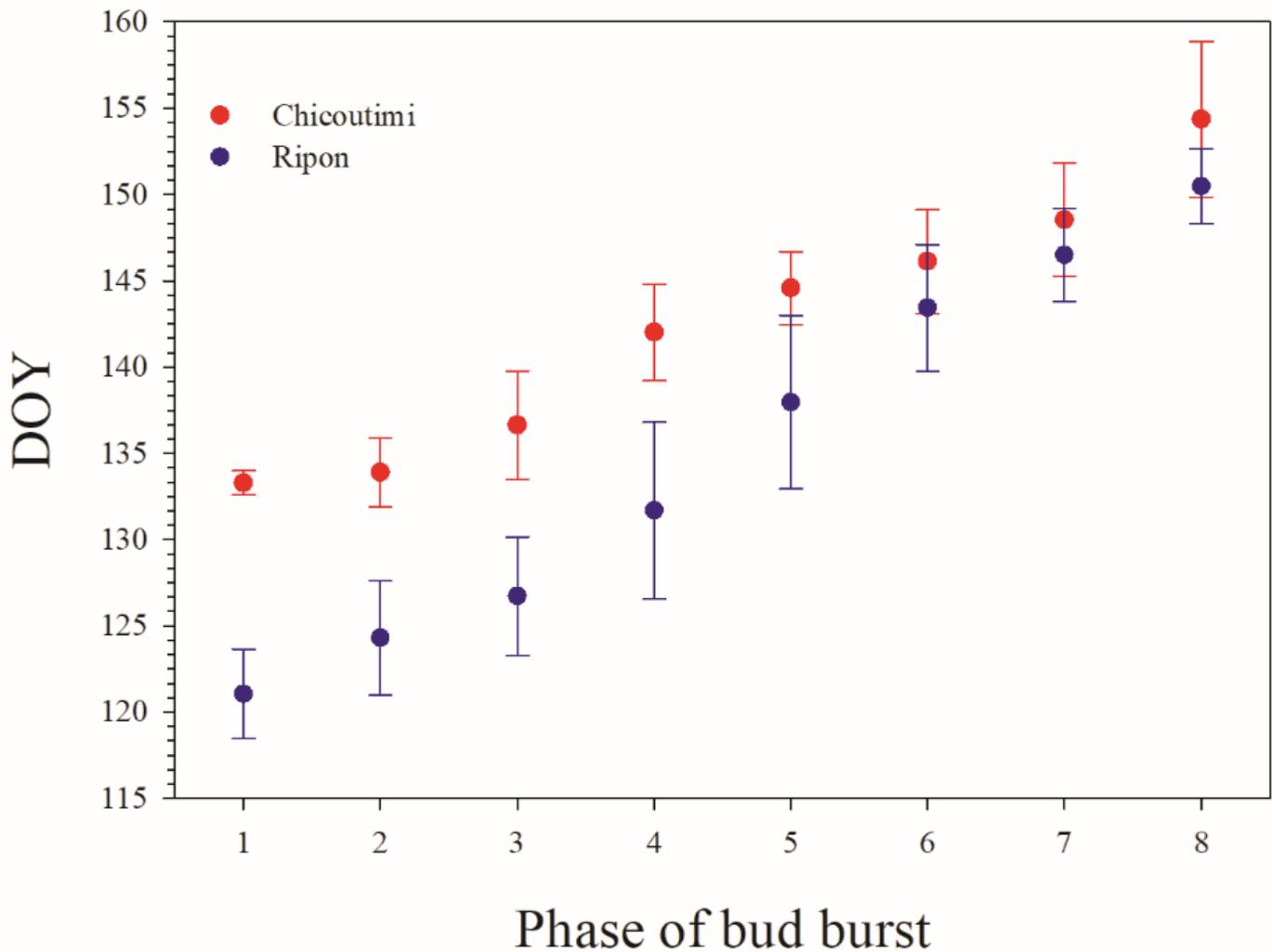


Figure 3

Occurrence of the different leafing phases of sugar maple in the two common gardens. Values are reported as average and standard deviation.

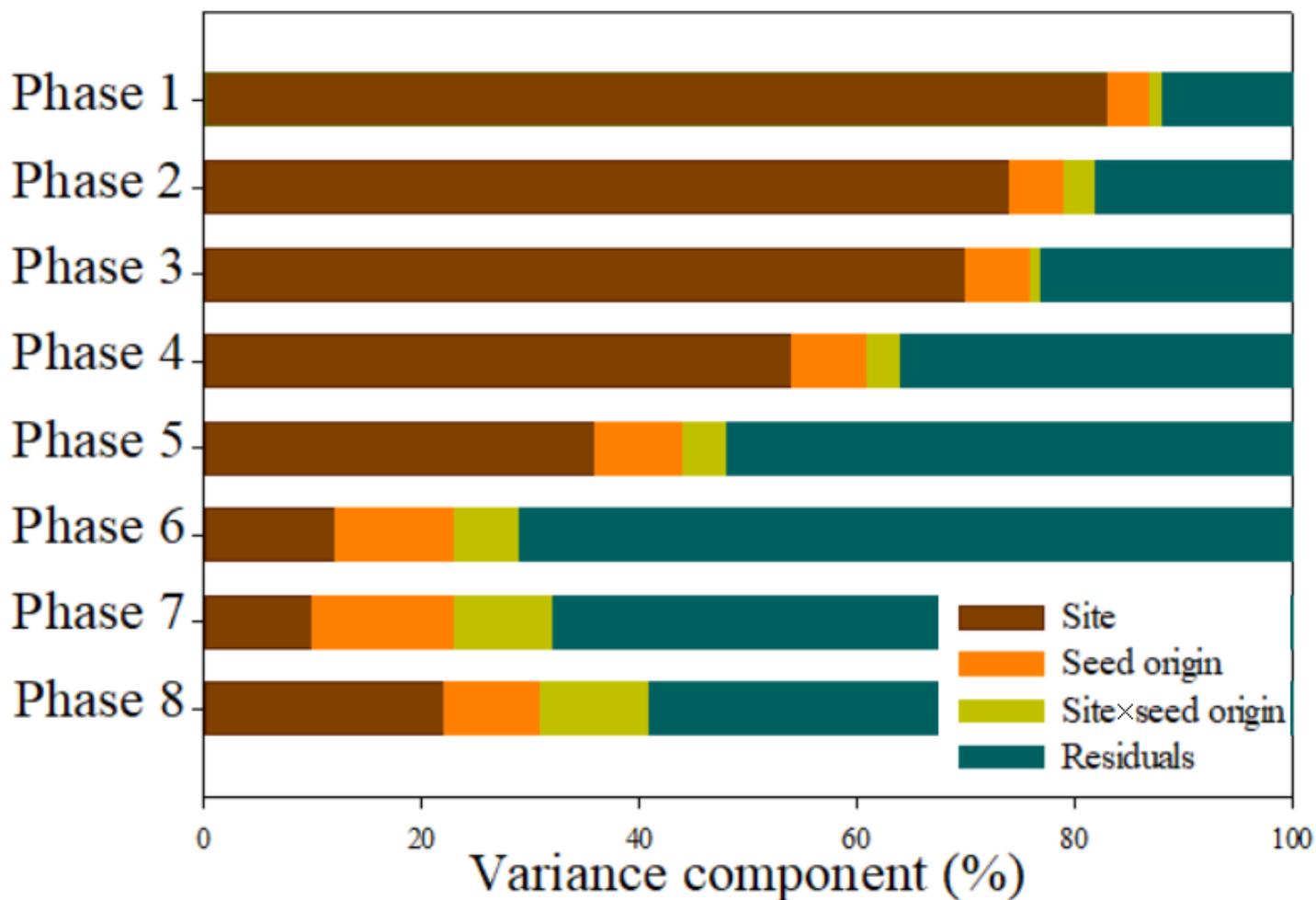


Figure 4

Relative contribution of the effects of site, seed origin and their interaction to the variance of bud phenology in sugar maple.

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