

# Spring Flowering Response to Climate Change between 1936 and 2006 in Alberta, Canada

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*In documenting biological responses to climate change, the Intergovernmental Panel on Climate Change has used phenology studies from many parts of the world, but data from the high latitudes of North America are missing. In the present article, we evaluate climate trends and the corresponding changes in sequential bloom times for seven plant species in the central parklands of Alberta, Canada (latitude 52°–57° north). For the study period of 71 years (1936–2006), we found a substantial warming signal, which ranged from an increase of 5.3 degrees Celsius (°C) in the mean monthly temperatures for February to an increase of 1.5°C in those for May. The earliest-blooming species' (Populus tremuloides and Anemone patens) bloom dates advanced by two weeks during the seven decades, whereas the later-blooming species' bloom dates advanced between zero and six days. The early-blooming species' bloom dates advanced faster than was predicted by thermal time models, which we attribute to decreased diurnal temperature fluctuations. This unexpectedly sensitive response results in an increased exposure to late-spring frosts.*

*Keywords: climate change, global warming, phenology, flowering, Canada*

**T**he scientific field of phenology, the study of the seasonal timing of life-cycle events, has seen a recent revival in light of climate change's growing prominence. Sparks and colleagues (2009) noted that the use of the term *phenology* in the scientific literature became seven times more common between 1990 and 2008. In documenting biological responses to global climate change, the Intergovernmental Panel on Climate Change has relied on phenology studies as compelling evidence that species and ecosystems respond to global climate change (Rosenzweig et al. 2007). Particularly for perennial plants in temperate zones, temperature exposure over time is the main driver for spring development, including the timing of bloom and leafout (Rathcke and Lacey 1985, Bertin 2008). This makes spring phenology one of the most sensitive, immediate, and easily observed responses to changing climate in temperate regions (e.g., Schwartz et al. 2006).

The use of phenology observations to document climate variability and climate change has a long history. Arakawa (1955, 1956) analyzed a long-term record of the dates of the annual cherry blossom festival in Japan that reached back to the ninth century. Remarkable phenology records covering more than two centuries also exist for European countries, starting with observations made by Linnaeus in the eighteenth century (Parmesan 2006). In a meta-analysis for Europe, Menzel and colleagues (2006) compiled an astonishing 125,000 time series recorded for more than 500 plant species in 21 countries.

Although a number of famous North American historical figures were involved in early systematic phenology

observations, including Thomas Jefferson, Henry David Thoreau, and Aldo Leopold (Stoller 1956, Miller-Rushing and Primack 2008), long-term records of phenology observation are scarce for North America as compared with Europe (Schwartz and Beaubien 2003). A notable analysis was carried out by Aldo Leopold's daughter N. L. Bradley and his son A. C. Leopold. They compared Aldo Leopold's 1935–1945 Wisconsin farm records (Leopold and Jones 1947) with data on 36 plant species collected in the same area from 1976 to 1998 (Bradley et al. 1999). Another major long-term observation effort is the phenology network established by Caprio (1957), in which the phenology of lilac (*Syringa vulgaris*) and honeysuckle cultivars (*Lonicera* spp.) was recorded with the help of local garden clubs in 12 western US states until 1994 (Cayan et al. 2001). A similar lilac–honeysuckle network, which still exists today, was established in 1959 in the northeastern US states and eastern Canadian provinces (Schwartz and Reiter 2000). However, there is a notable lack of phenology data for western Canada and Alaska, where the change in the spring warming signal over the last 50 years has been most pronounced globally (Rosenzweig et al. 2007).

Besides being a documentation of global change, trends in plant phenology can reveal important ecological consequences associated with climate change (Parmesan 2006, Cleland et al. 2007). Plant populations are finely tuned to local frost-risk environments at the beginning and end of the growing season, and phenological traits are usually highly heritable and are often subject to strong selection

pressures (Campbell and Sugano 1975, Vitasse et al. 2009, Li et al. 2010). The timing of spring plant development balances the need to avoid damage due to late-spring frosts with a maximization of the use of the available growing season in competition with other species (Lechowicz 1984, Leinonen and Hänninen 2002). Therefore, plants at higher northern latitudes and at high elevation break bud relatively early; that is, the need to utilize the growing season takes precedence over avoiding late-spring frost damage. This has been documented in many common garden studies for widespread plant species (reviewed in Li et al. 2010).

The timing of spring development in virtually all temperate perennial plants is primarily controlled by temperature (Rathcke and Lacey 1985, Hunter and Lechowicz 1992). Plants require a certain amount of exposure to warm temperatures before leafout or flowering occurs. Exposure to warm temperatures over time can be measured in degree days, which is the sum of the average daily temperatures above a base value. A common base temperature is 5 degrees Celsius (°C), which is widely used to calculate growing degree days in agriculture. For a given species, this amount of warmth over time, referred to as the *required heat sum*, is nearly constant and can be used to predict bloom times from daily temperature records in what is called a *thermal time model* (Bertin 2008). The required heat sum for spring development is a genetically controlled adaptive trait (Leinonen and Hänninen 2002). Heat sum accumulation allows plants to respond to an unpredictable onset of the growing season, which can easily vary by a month in northern latitudes.

If spring development were exclusively driven by exposure to warm temperatures, climate change would not be expected to affect the match of plant development with the available growing season. However, additional factors are known to modulate the timing of spring development. Photoperiod may delay bud break if warm temperatures arrive unusually early (Menzel et al. 2005). Some plants also require a certain amount of exposure to cool temperatures following bud set in the fall before they start development in response to warm spring temperatures. This is referred to as a *chilling requirement* and is measured by summing the exposure to moderately cool temperatures, typically between 0°C and 10°C. The chilling requirement is thought to guard plants from prematurely breaking bud during midwinter thaws. In both cases, climate warming would be expected to delay the spring response. Plants may be constrained by photoperiod effects that prevent early development, or in warmer regions, they may not receive sufficient exposure to cold temperatures to release them from dormancy (Bertin 2008).

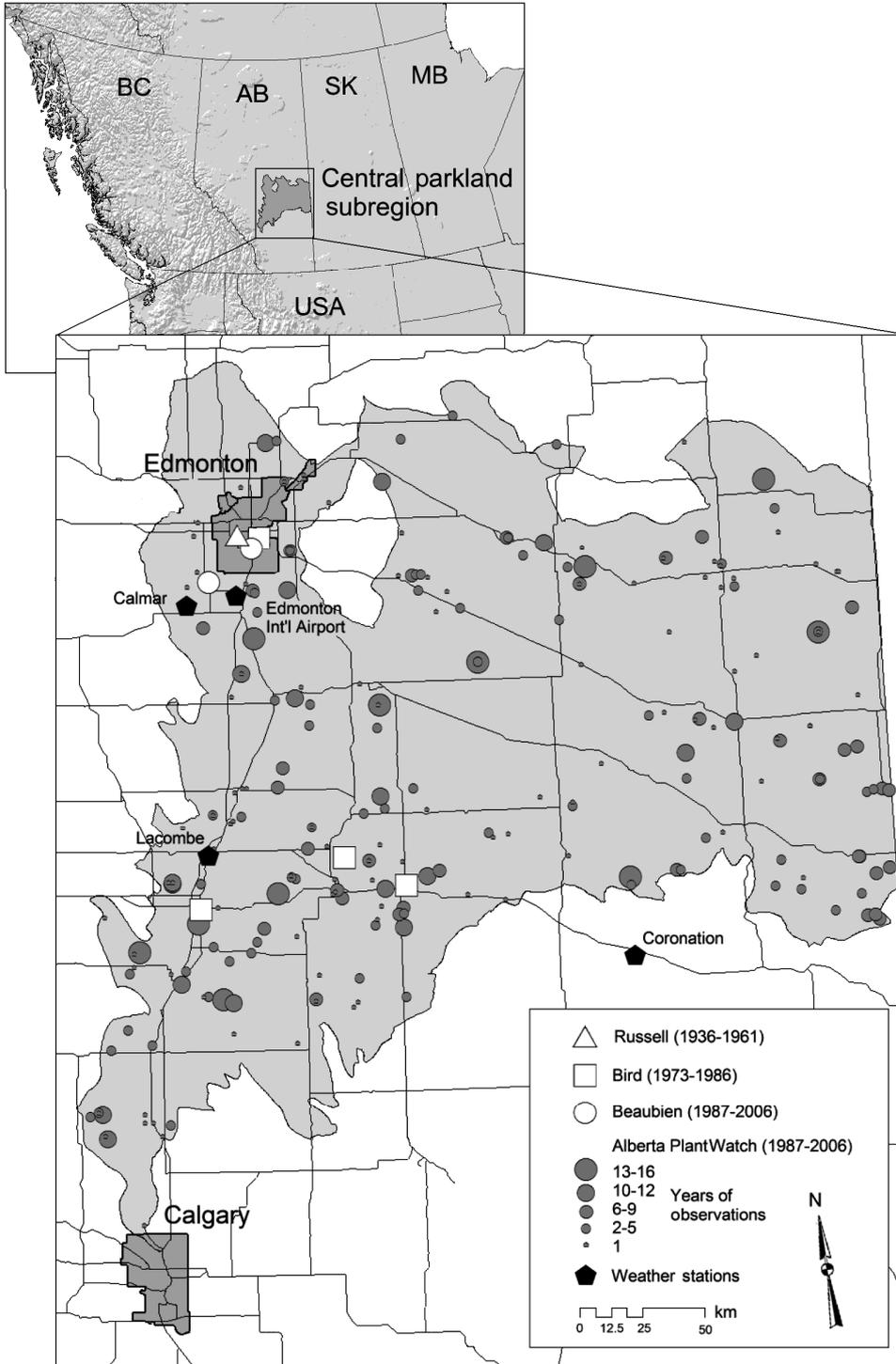
Another factor that affects spring phenological response at high latitudes and high elevation is the prevalence of snow (Inouye and Wielgolaski 2003, Wielgolaski and Inouye 2003). A deep spring snowpack further shortens the growing season, and once the snow has melted, the plant response is often immediate, suggesting very low heat sum

requirements, and making the release from snow a primary driver of spring phenology. This also has important implications for the effects of climate change. A smaller snowpack due to either higher temperatures or less precipitation would lead to an earlier release from snow, an earlier start of plant development, and potentially higher frost exposure (Inouye 2008).

In the present article, we report the results from spring flowering observations conducted over approximately seven decades (1936–2006) in Alberta, western Canada. We analyzed the first-bloom dates for seven plant species that come into flower in a temporal sequence between early April and June. The first objective of this study was to attempt to provide evidence of a plant response to global climate change for a higher-latitude location in western North America, a region for which long-term data are scarce. Second, we asked whether phenology trends correspond to observed temperature trends according to spring thermal time models or, alternatively, whether other factors influence spring development, which would potentially lead to altered sequences of bloom time. Finally, we investigated whether shifts in bloom time have led to changes in the exposure of species to late-spring frosts.

### Phenology observations in central Alberta

We evaluated observations from a phenology network across the central parkland of Alberta (figure 1). This ecological subregion covers approximately 50,000 square kilometers and is situated between the boreal forest to the north and the warmer and drier grasslands to the south. The native vegetation consists of open forests dominated by two poplars (*Populus tremuloides* Michx. and *Populus balsamifera* L.), white spruce (*Picea glauca* [Moench] Voss), and birch (*Betula* spp.), as well as prairie vegetation found under drier microsite conditions. However, much of the native vegetation has been converted to agricultural use because the area has some of the best soils in Canada. Intensive phenology observations began in 1936 with a program by Agriculture Canada, in which the timing of wheat development and the bloom times for 50 native plant species were recorded over 26 years. The purpose of this program was to identify indicator events to guide the timing of agricultural activities (Russell 1962). This program ended in 1961, which resulted in a data gap of 11 years before botanist Charles Bird initiated a new research program, which tracked the bloom times for 12 native species between 1973 and 1986. The data were collected by a network of citizen scientists (Bird 1983), supplemented by Bird's own observations (figure 1). This network was extended by EB in 1987, and in its current form, the volunteer observers record data for one or more of 25 species ([www.plantwatch.fanweb.ca](http://www.plantwatch.fanweb.ca)). Since 1987, this network has collected data from approximately 650 observers, with up to 240 observers reporting each year. The plant species for this phenology network were selected primarily on the basis of the plants' wide distribution and short bloom period in



**Figure 1.** Central parkland study area in Alberta, western Canada. The figure indicates the location of long-term weather stations and the locations of phenology observations. The white symbols indicate long-term observations. For the Alberta PlantWatch network, the size of the circles indicates the length of data collection by a volunteer.

spring, the ease of their identification by citizens, and the lack of similar-looking species. For additional background on these data series, see Beaubien and Johnson (1994) and Beaubien and Freeland (2000).

phenology data from the greater Edmonton area. Edmonton's human population has grown at an exponential rate to over one million from 85,000 at the beginning of this research (Statistics Canada 2010). It is therefore possible

In the present study, we evaluated the dates of the first bloom for several plant species. *First bloom* was defined as a plant stage at which the first flower buds had opened in an observed tree or shrub or in a patch of smaller plants. We requested that the observers report on plants that were situated in flat areas away from heat sources such as the walls of houses. Observers were asked to select plants that approximately represented the average bloom time for that species in their area (i.e., that were not the first or last of that species to bloom). Therefore, our first-bloom data do not represent the earliest-blooming individuals of a population (as in Miller-Rushing et al. 2008). Rather, they represent a developmental stage sampled to represent a local population. Generally, the first-bloom stage is the simplest to observe and yields more temporally precise data than later bloom stages, which can be harder to estimate. Because many of the data (e.g., those collected between 1987 and 2006) were compiled from multiple individual plant observations, we used the mean annual bloom date from all available points in the central parkland. The annual first-bloom dates were categorized by species and year for all three data sets and were used for statistical analysis and graphical presentation. Except for the first data set (collected between 1936 and 1961; Russell 1962), we excluded

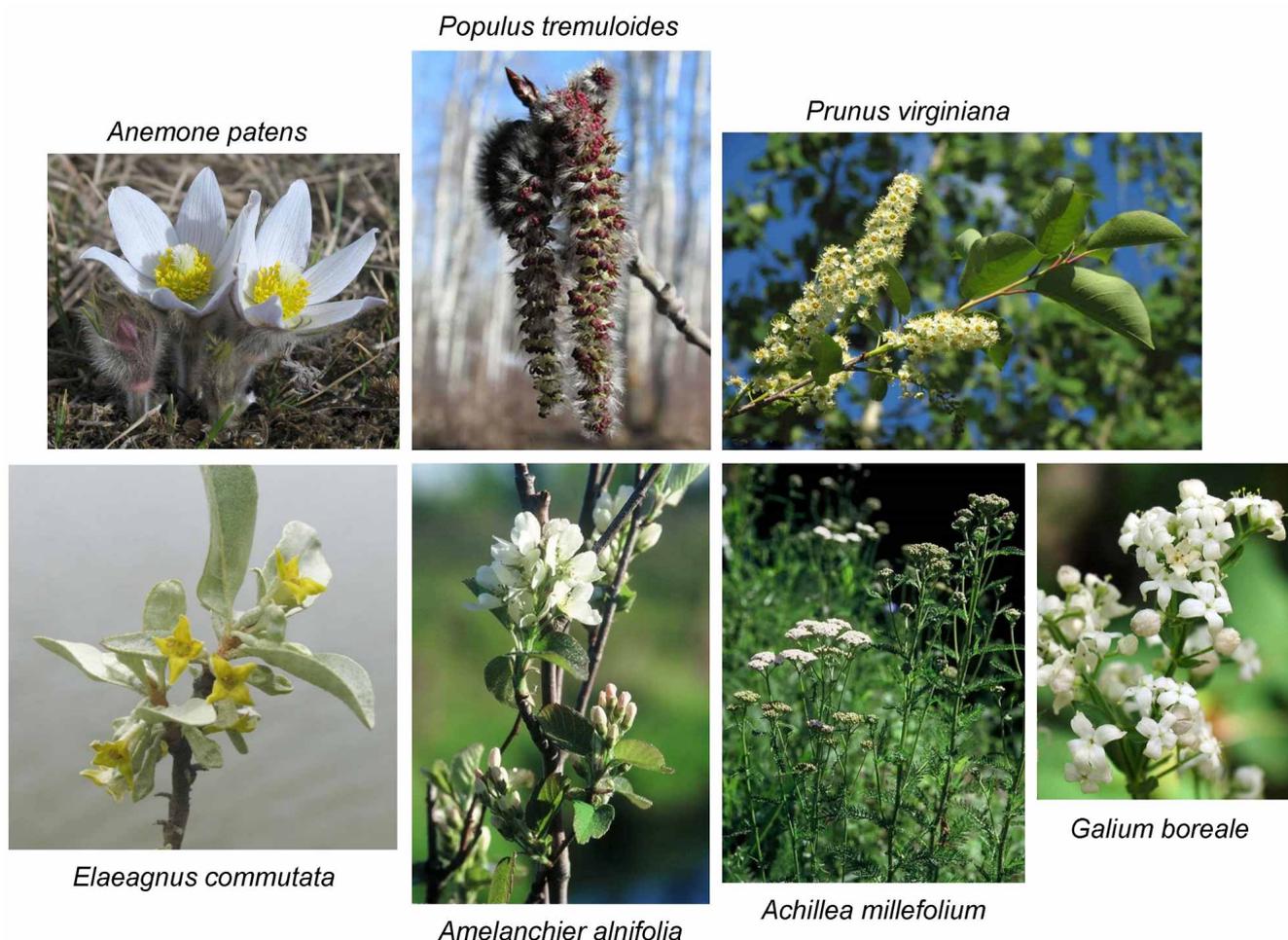
that urban heat-island effects on temperature may confound data on climate-change trends (e.g., Roetzer et al. 2000).

The three observation programs (those of Russell [1962], Bird [1983], and Beaubien [Beaubien and Johnson 1994, Beaubien and Freeland 2000]) included the same four woody and three herbaceous (nonwoody) plant species (figure 2). The first species to bloom is the prairie crocus (*Anemone patens* L.), which is found in grasslands throughout the Northern Hemisphere and blooms soon after a snowmelt. Usually blooming within two days of the prairie crocus is the trembling aspen (*P. tremuloides*), one of the most common and widely distributed tree species in North America. It is the first tree in Alberta to shed pollen and to produce leaves in spring. About 25 days later, saskatoon, or serviceberry, (*Amelanchier alnifolia* Nutt.) blooms. Saskatoon is a widespread tall woody shrub with edible berries that were the most important plant food for the prairie Blackfoot First Nations. The remaining four species follow in approximately eight-day intervals, starting with the choke

cherry (*Prunus virginiana* L.), a tall woody shrub that is also widespread throughout North America. The wolf willow (*Elaeagnus commutata* Bernh. ex Rydb.), or silverberry, is a nitrogen-fixing, medium-sized shrub with a short, well-defined bloom period and an overpowering smell that aids in correct identification. The northern bedstraw (*Galium boreale* L.) is another widely distributed and easily identified herbaceous species. The last species in this sequence is the yarrow (*Achillea millefolium* L.), perhaps one of the best known and most widely distributed herbaceous species in the world. In this section, we followed the scientific nomenclature of Moss (1983).

### Climate and phenology trends

We used daily minimum, maximum, and mean temperature data obtained from the Adjusted Historical Canadian Climate Database (AHCCD 2009) to analyze climate trends. This database includes four weather stations with long-term records for the study area (figure 1): Edmonton

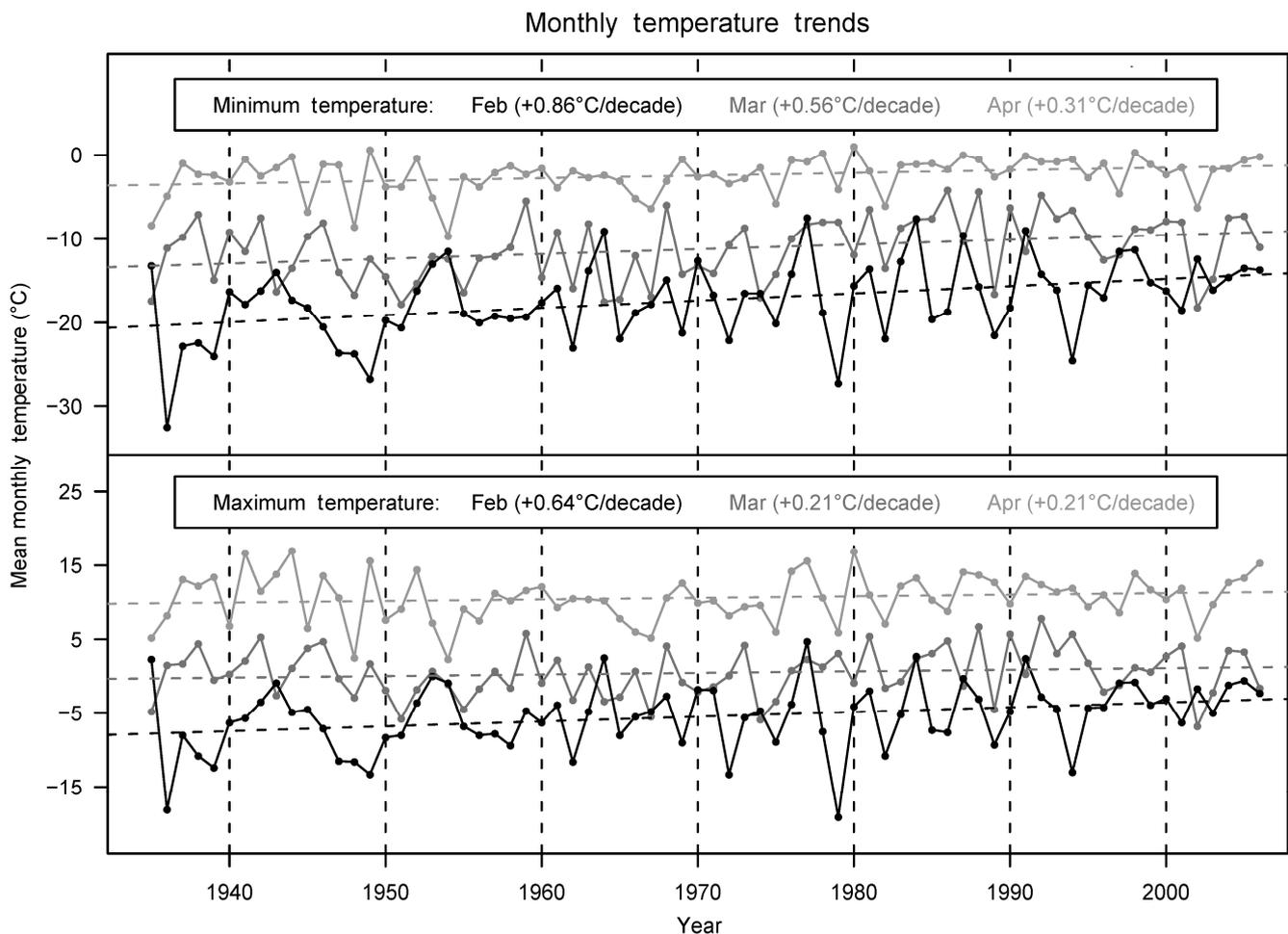


**Figure 2.** The species included in the study were prairie crocus (*Anemone patens* L.); trembling aspen (*Populus tremuloides* Michx.); choke cherry (*Prunus virginiana* L.); wolf willow (*Elaeagnus commutata* Bernh. ex Rydb.), or silverberry; saskatoon (*Amelanchier alnifolia* Nutt.), or serviceberry; yarrow (*Achillea millefolium* L.); and northern bedstraw (*Galium boreale* L.). Photos by Linda Kershaw.

International Airport (ID #3012205), which is well outside the city of Edmonton; Lacombe (ID #3023722); Calmar (ID #3011120); and Coronation (ID #3011887). To visualize temperature trends and to compare station records, we also calculated the mean monthly minimum, the mean monthly maximum, and the mean temperature values for February, March, April, and May from the daily data. In addition, we generated interpolated monthly data following the method of Mbogga and colleagues (2009) for the central parkland ecoregion. The interpolated climate data and station data suggest that the central parkland ecoregion is climatically very homogenous. The mean monthly temperatures for February, March, and April for the 1961–1990 normal period differ by less than 1°C between any two of the four weather stations and among the grid cells of the interpolated surface. The average correlation coefficient between pairs of stations is .97 for the mean monthly temperatures from February through May. Because of the climatic homogeneity of the study area, we used the mean climate values from the four weather stations for subsequent analysis, which matches the data preparation of phenology observations as regional averages for the central parkland.

We observed a substantial warming trend between 1936 and 2006 that was most pronounced in late winter and early spring (figure 3). For the 70-year period of this research, the slope of a linear regression equates to a 5.3°C increase in the mean February temperature, a 2.7°C increase in the mean March temperature, and a 1.8°C increase in the mean April temperature. These trends were even more pronounced in the mean monthly minimum temperatures (6.0°C, 3.9°C, and 2.2°C for February, March, and April, respectively), whereas the mean maximum temperature changes over the study period were 4.5°C, 1.5°C, and 1.5°C. A Mann–Kendall test for identifying trends in time-series data following the method of Hipel and McLeod (1994) revealed that the warming trends for the monthly temperatures from February to April were statistically significant at  $\alpha = .05$  (table 1).

The annual sequence of the species' first-bloom dates was fairly consistent between years (figure 4a). The plants responded to warming temperatures by blooming earlier in spring, with the most pronounced changes in the earliest-blooming species (*A. patens* and *P. tremuloides*). These species' flowering dates advanced by approximately two weeks, whereas the later-blooming species' flowering dates advanced

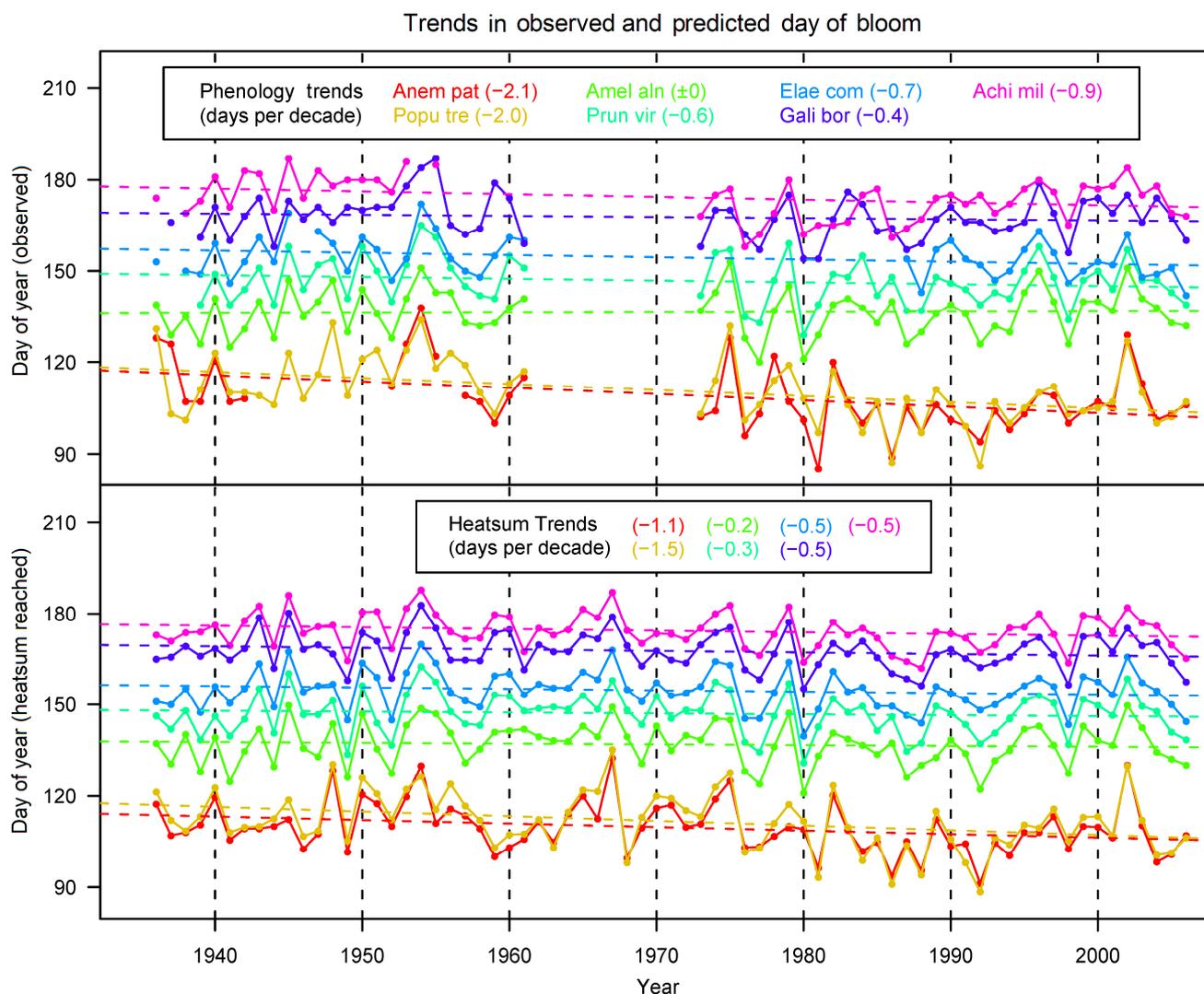


**Figure 3.** Temperature trends for the central parkland study area for the change in the mean monthly minimum temperature (in degrees Celsius) and the change in the mean monthly maximum temperature.

**Table 1. Mann–Kendall test statistics for time-series trends in minimum, maximum, and mean monthly temperature (shown in figure 3).**

Month	Minimum temperature			Maximum temperature			Mean temperature		
	Temperature change (°C per decade)	Mann–Kendall statistic ( $\tau$ )	$p(>\tau)$	Temperature change (°C per decade)	Mann–Kendall statistic ( $\tau$ )	$p(>\tau)$	Temperature change (°C per decade)	Mann–Kendall statistic ( $\tau$ )	$p(>\tau)$
February	0.86	0.31	.0001	0.64	0.28	.0004	0.75	0.28	.0003
March	0.56	0.21	.0052	0.21	0.07	.1854	0.39	0.15	.0365
April	0.31	0.18	.0157	0.21	0.07	.1928	0.26	0.12	.0756
May	0.05	0.10	.1275	0.00	0.04	.5874	0.02	0.04	.3010

°C, degrees Celsius



**Figure 4. (a) Trends in observations of first bloom for seven species. The species names are abbreviated to the first four letters of the genus and the first three letters of the species name provided in figure 2. (b) The predicted day of first bloom from a thermal time model (the best model is highlighted in bold in table 3).**

between zero and six days over the study period. A Mann–Kendall test also confirmed the advanced blooming in the earliest-blooming species as statistically significant (table 2).

This result corresponds to the observed temperature changes, with considerable warming in late winter but minimal warming in late spring.

**Table 2. Mann–Kendall test statistics for time-series trends in first-bloom dates for seven plant species, expressed in number of days per decade shift to earlier bloom time.**

Species	Change in bloom time (days per decade)	Mann–Kendall statistic ( $\tau$ )	$p(<\tau)$
<i>Anemone patens</i>	–2.1	–0.26	.0039
<i>Populus tremuloides</i>	–2.0	–0.29	.0008
<i>Amelanchier alnifolia</i>	0.0	0.03	.6181
<i>Prunus virginiana</i>	–0.6	–0.09	.1759
<i>Elaeagnus commutata</i>	–0.7	–0.16	.0735
<i>Galium boreale</i>	–0.4	–0.03	.3735
<i>Achillea millefolium</i>	–0.9	–0.09	.1673

Note: See figure 4a.

Trends toward an earlier onset of spring phenology in the Northern Hemisphere are well documented in the literature. In a meta-analysis for the Northern Hemisphere, Root and colleagues (2003) revealed an average three-day advance per decade in tree phenology, with somewhat more pronounced trends at higher latitudes. For Western Europe, Menzel and colleagues (2006) and Schleip and colleagues (2009) analyzed phenology time series of at least 30 years between 1955 and 2000. They found that changes in the spring phenology of plants were most pronounced in central and western maritime Europe, advancing around 3.5 days per decade. These changes appear to be larger than our observed changes for our earliest-blooming species (which advanced approximately two days per decade). However, the difference arises mainly from the observation period. For example, in a long-term study of UK plant communities, Amano and colleagues (2010) found approximately the same 3.5 days per decade rate of change as did Menzel and colleagues (2006) over the last 30 years. Conversely, the rate of change over the 70 years corresponding to our study showed an advance of only approximately one day per decade for the data from Amano and colleagues (2010), because most of the observed warming at their study site occurred over the last 30 years. Our observation of a total advance of 14 days for *A. patens* and *P. tremuloides* over 70 years appears to be on the high end of changes observed in the Northern Hemisphere.

### Thermal time models of spring development

Thermal time models use daily temperature data to predict the timing of bud break or flowering. Daily temperatures are, however, not directly used as predictor variables. Instead, daily temperature values are integrated over time by adding daily temperature measurements. The derived predictor variable for bud break or flowering is the date at which the temperature sum reaches a certain value (the required heat sum). De Réaumur (1735) was the first to establish the principle of thermal time and the concept of degree days as predictors for plant development. Degree days are calculated as the sum of

the daily average temperature values from a chosen start date (often arbitrarily set as 1 January) and a threshold value (often 0°C to 5°C for early spring-blooming species). This summation continues up to the day of a phenology event, yielding a required heat sum for the observed event.

This classical thermal time model has been modified in various ways to account for the nonlinearity of the physiological response to temperature (for a review, see Bonhomme 2000). Other modifications include accounting for the chilling requirements of plants before temperature accumulation begins or for additional environmental factors (for a review, see Chuine et al. 2003). Nevertheless, the simple linear model has proven to be surprisingly accurate, often having just one variable parameter: minimum temperature threshold. This parameter bounds the lower end of the temperature range that is assumed to be approximately linearly correlated with a spring physiological response (Bonhomme 2000). Sometimes, start dates of heat sum accumulation other than 1 January are tested in order to approximately account for dormancy release or photoperiod effects (e.g., Wielgolaski 1999). Complex mechanistic or statistical models often yield only minor improvements—if any—over the classical thermal time model, particularly for studies that are not carried out in controlled environments (e.g., Hannerz 1999, Schaber and Badeck 2003, Linkosalo et al. 2006).

In figure 4b and table 3, we show the results from a classical thermal time model applied to our data. The development of a thermal time model involves the selection of a base temperature for degree-day calculations—for example, 0°C. The next step is to calculate the required heat sum for an observed phenology event to occur. This required heat sum is a mean value based on the phenology events of a species observed over multiple years that can be estimated with a standard error (SE; see table 3). With a species-specific required heat sum value, we can now use daily temperature data to predict a bloom time for each year (figure 4b). The correlation between the observed bloom dates in each year (figure 4a) and the bloom date predicted by the thermal time model (figure 4b) serves as a measure of model fit. The model fit may be improved by modifications of base temperatures or start dates.

We tested a wide range of base temperatures for degree-day calculations from –10°C to 10°C, in 1°C intervals. Furthermore, we tested multiple start dates for temperature accumulation (1 January, 1 March, and 31 March) in order to account for possible unmet chilling requirements. The best thermal time model—the one with the highest correlation between the observed and the predicted flowering dates—was obtained with threshold values between –3°C and 3°C (bold correlation coefficients in table 3). This is a fairly typical result for northern temperate and boreal plant species, which usually have optimal threshold parameters between 0°C and 5°C (e.g., White 1995, Hannerz 1999). As was expected for a northern environment, later start dates did not improve the correlations, suggesting that species' chilling requirements were met before winter. We therefore report only the statistics for a start date of 1 January in table 3.

**Table 3. Correlations between flowering date and thermal time for different base temperature values for heat sum accumulation.**

Species	Years of recorded data	Heat sum			Base temperature (°C)							MAE (days)
		HS <sub>0</sub> (°C)	HS (°C)	SE	-3	-2	-1	0	1	2	3	
<i>Anemone patens</i>	50	94	187	9.6	<b>.81</b>	.80	.79	.78	.75	.72	.68	3.9
<i>Populus tremuloides</i>	60	103	202	6.4	<b>.90</b>	.89	.88	.88	.86	.84	.81	4.5
<i>Amelanchier alnifolia</i>	60	303	172	3.1	.84	.86	.87	.89	.90	.91	<b>.92</b>	1.6
<i>Prunus virginiana</i>	57	419	258	3.8	.84	.86	.87	.89	.90	.90	<b>.91</b>	2.4
<i>Elaeagnus commutata</i>	44	511	385	7.0	.75	.76	.78	.79	.80	<b>.81</b>	.81	3.5
<i>Galium boreale</i>	58	690	467	6.3	.70	.72	.74	.75	.75	.76	<b>.77</b>	2.1
<i>Achillea millefolium</i>	52	782	696	8.9	.69	.71	.72	.73	<b>.74</b>	.73	.72	2.2

Note: The threshold value for the best model (highest correlation) is shown in bold.

°C, degrees Celsius; HS, heat sum for the best model; HS<sub>0</sub>, heat sum for a threshold of 0°C, provided for comparison of thermal time requirements across species; MAE, mean absolute error of the observed versus the predicted bloom time; SE, standard error

Correlation coefficients are a good measure to use in assessing statistical error, but they do not detect statistical bias (systematic over- or underprediction). We therefore validated the thermal time model using a second statistical measure: mean absolute error (MAE). MAE is calculated as the absolute difference between the observed and predicted bloom dates. We carried out an independent cross-validation using a temporal split of the temperature and phenology data. The first two-thirds (1936–1986, with approximately 40 years of data) were used for the development of the thermal time model, and the last third (1987–2006) was used for model validation.

Generally, the classical thermal time model appears to be very accurate in predicting the mean bloom dates of the species in the central parkland (table 3). The MAE values in predicting bloom time in the independent cross-validation ranged from 1.6 to 4.5 days. The species with the largest MAE values in table 3 were the earliest-blooming species: *A. patens* and *P. tremuloides*. For these species, the predictions were biased, underpredicting the rate of change in bloom time (compare figure 4a and 4b).

### Observed versus predicted phenology trends

In an attempt to explain the discrepancy between the observed and predicted trends in *A. patens* and *P. tremuloides*, we used a multiple regression approach in order to incorporate other climatic and environmental factors (see equation 1 in Chuine et al. 2003). The environmental factors that we tested include the amount of winter precipitation that fell as snow, the depth of snowpack at the end of February and March, and several dryness indices. We

also checked for the effects of chilling requirements in the previous fall, with chilling degree days calculated between the upper and lower thresholds of 0°C and 5°C and 2°C and 8°C, following the method of Linkosalo and colleagues (2006). None of these additional factors could account for a significant portion of the variance that was not already explained by the thermal time model (data not shown). A nonlinear, Q<sub>10</sub>-based thermal time model following the method of Bonhomme (2000) yielded model accuracies for all species (measured as *r*<sup>2</sup> between the observed and predicted events and as the SE of heat sum) that were similar to previous results (figure 4b). However, they actually increased the discrepancy between the observed and predicted temporal trends for the early-blooming species by a small amount (data not shown).

A possible remaining explanation is that spring phenology is not only a function of mean daily temperatures; it is also influenced by the amplitude of diurnal temperature variations. Karl and colleagues (1993) were the first to demonstrate that global minimum temperature increased faster than maximum temperature, resulting in a significant decrease of diurnal temperature variation, which was subsequently confirmed by Easterling and colleagues (1997). This differential warming pattern in minimum and maximum temperatures clearly applies to our study area as well, where the minimum night temperatures in March increased more than twice as fast as the daily maximum temperatures (figure 3, table 1). We therefore hypothesize that the increase of the minimum night temperatures relative to the mean daily temperatures used in the heat sum model results in a more rapid heat sum accumulation.

Although heat sum accumulation calculated from minimum night temperatures is not biologically reasonable because it does not incorporate daytime temperature exposure, we explored this option as well. The result is a relatively poor model fit ( $r = .79$  for *P. tremuloides*), but the flowering advance over time was predicted more accurately (14 days observed versus 13 days predicted over the study period). It makes adaptational sense that the minimum temperature values (which could represent damaging frost events) modulate daytime thermal time accumulation to control spring development. This would allow plants to fine-tune spring development for microsites with different diurnal temperature variation but may also increase the exposure of *P. tremuloides* and *A. patens* to late-spring frosts under climate change.

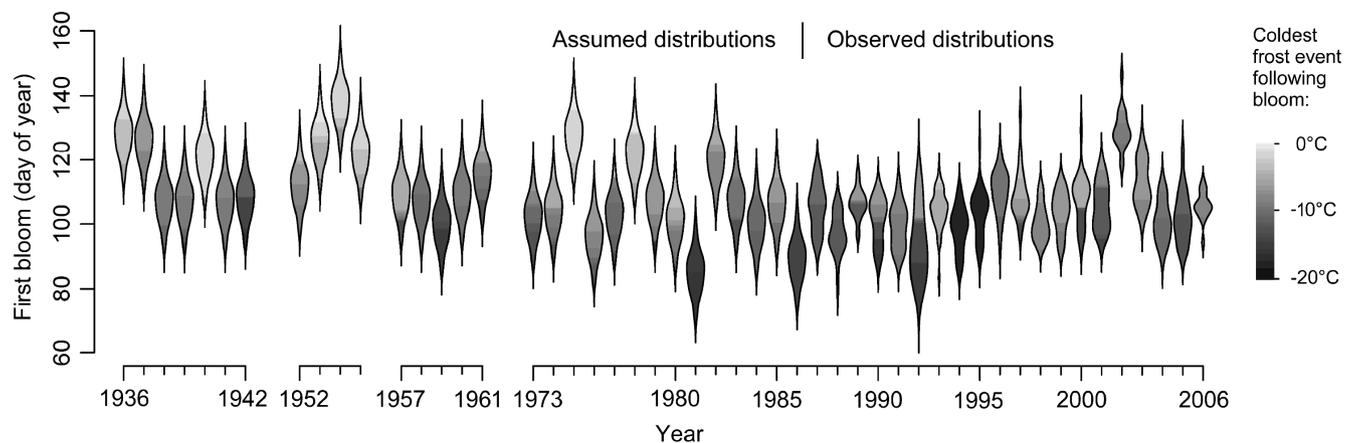
### Exposure to late-spring frost

Late-spring frosts of  $-10^{\circ}\text{C}$  occurred earlier, at a rate of 0.7 days per decade, and very severe spring frosts of  $-20^{\circ}\text{C}$  occurred earlier, at a rate of 1.1 days per decade over the study period (data not shown). This is a considerably slower rate than the advance of bloom times for the early-blooming species, which occurred at a rate of approximately 2 days per decade (figure 4a). This discrepancy raises the question of whether early-blooming species might be exposed to increased risks of late-spring frosts because of climate change.

To answer this question, we compared the incidence of late-spring frost events with the timing of first bloom. In figure 5, we show the variance of bloom times observed across a population sample of *A. patens* for different years by means of a special form of boxplot, the so-called *violin plot*, which reveals the frequency of bloom time for different dates. This plot quantifies the bloom dates of the sampled population (the width of the violin plot points indicates frequency, the number of reported observations with that date). It also shows the latest dates of spring frost events ranging from  $0^{\circ}\text{C}$

to  $-20^{\circ}\text{C}$  (represented by the gradient). To give an example, in 1994 and 1995, there were frost events of  $-20^{\circ}\text{C}$  as late as 28 and 30 April (days 118 and 120, respectively). That means that virtually all of the reported flowering individuals were exposed to these extreme frost events. As a contrasting example, in 2000, we had a  $-12^{\circ}\text{C}$  event that occurred on 14 April (day 104). This affected only the early-blooming portion of the population. Most individuals bloomed after that late frost event and were exposed only to a  $-4^{\circ}\text{C}$  frost that occurred as late as day 133 (13 May). In figure 5, trends toward an earlier bloom would be represented by the violin plot points being located higher on the left side than on the right side. Higher frost exposure experienced by blooming populations would be visible as darker colors toward the right side. Note that we have population-level information from many observers of the PlantWatch Alberta network only since 1987. Before that date, we assume a normal distribution around the known annual average reported by Russell (1962) and Bird (1983).

In the case of *A. patens*, we can see a slightly increased exposure of blooming populations to frost events over time, with overall darker shades toward the right side of figure 5. To test whether this trend is statistically significant, we cannot directly use the distributions shown in figure 5, since we lack population-level data from before 1987. Instead, we analyzed trends in the value of the coldest frost event following the average bloom times shown in figure 4a for each year (table 4; later-blooming species that were not exposed to frost were excluded). For example, *A. patens* individuals with an average bloom time were exposed to colder spring frost events, at a rate of  $-0.57^{\circ}\text{C}$  per decade. This means that frost events to which blooming plants were exposed were on average  $4^{\circ}\text{C}$  colder at the end than at the beginning of the study period. This trend was not significant for any other species at an  $\alpha$  level of .05. However, two other early-blooming species showed similar trends toward increased exposure to



**Figure 5.** The distribution of the day of the year when flowers appear in *Anemone patens* individuals. The width of the points in this form of boxplot indicates the frequency of reported observations. The gradient indicates the severity of frost events to which blooming individuals are exposed, with the lighter part of the gradient representing less severe frost events. We have population-level data available only since 1987. Before that date, we assume a normal distribution (which is used only for visualization in this figure).

**Table 4. Mann–Kendall test statistics for time-series trends in the value of the coldest frost event following average bloom time, expressed in degrees Celsius change per decade.**

Species	Temperature change (°C per decade)	Mann–Kendall statistic ( $\tau$ )	$p(<\tau)$
<i>Anemone patens</i>	−0.57	−0.20	.0231
<i>Populus tremuloides</i>	−0.44	−0.15	.0521
<i>Amelanchier alnifolia</i>	−0.13	−0.06	.0671
<i>Prunus virginiana</i>	−0.01	0.01	.4909

frost, and trends of this magnitude or larger would arise by random chance only once in 19 times for *P. tremuloides* or once in 16 times for *A. alnifolia*.

This paradoxical result of increased frost risk with climate warming differs from the results of comparable studies at lower latitudes. Scheifinger and colleagues (2003) observed that frost risks generally decreased, because the retreat of late frosts outpaces the advance of spring development. However, the low heat sum requirements of species from environments with short growing seasons results in a finely tuned adaptive balance between avoiding spring frost and using the available growing season (Li et al. 2010). Earlier snowmelt due to higher temperatures or lower winter precipitation may affect this balance in high-elevation environments (Inouye 2008). In our study, at relatively high latitude, we excluded snow as a factor that can explain the unexpectedly sensitive phenological response of *A. patens* and *P. tremuloides* to warming trends. Instead, changes in diurnal temperature fluctuations may be responsible for a faster advance in bloom dates than can be explained by standard thermal time models.

Although this explanation is speculative, it could guide future experimental research toward the development of improved thermal time models that take diurnal temperature fluctuations into account. Regardless of whether diurnal temperature variations are the ultimate cause of the discrepancy between the observed and predicted trends, our results suggest that projections of phenology response into the future, although they are important (e.g., Leinonen and Kramer 2002), should be made with caution. Models that explain interannual variation of plant response very well over a limited observation period may not always provide reliable long-term projections. In the case of *P. tremuloides* and *A. patens*, it appears that we would underpredict climate change response by 23% and 44%, respectively, with a standard thermal time model.

## Conclusions

In this study, we documented considerable advances in phenology over time that were driven by what we perceive as astonishing warming trends in spring temperature. Particularly in March, we also found large changes in diurnal temperature fluctuations (the average daily minimum temperatures increased 2.7 times faster than the daily maximum tempera-

tures in this month). The phenology response of two early-blooming species—*A. patens* and *P. tremuloides*—appears to be unexpectedly sensitive to these temperature changes. Their bloom times changed twice as fast as did the frost events, thus shifting their bloom period closer to the receding winter and increasing the danger of damage from late-spring frost.

The database that we analyzed was assembled as a collaborative effort among university biologists, government researchers, and over 650 members of the general public. This effort has both harnessed the energy of concerned citizens and provided them with biological insights and a raised awareness of climate-change issues in Alberta. Besides documenting a biological response to global climate change, citizen contributions are invaluable for the validation of remote-sensing data and the calibration of carbon uptake models in terrestrial ecosystems (Badeck et al. 2004). In conclusion, we would like to encourage interested readers to join local phenological networks that make this research possible. Links to local networks can be found at [www.plantwatch.ca](http://www.plantwatch.ca) for Canada and [www.usanpn.org](http://www.usanpn.org) for the United States.

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