Int. J. Plant Sci. 177(8):661–670. 2016.

1058-5893/2016/17708-0002$15.00 DOI: 10.1086/687984

CANADIAN ARCTIC ARCHIPELAGO CONSPECIFICS FLOWER EARLIER IN THE HIGH ARCTIC THAN THE MID-ARCTIC

Zoe A. Panchen[1,]* and Root Gorelick*

*Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada

Editor: Michele R. Dudash

Premise of research. The Canadian Arctic Archipelago is experiencing unprecedented climate change with temperatures rising at a rate that is twice the global average. The rapidly rising temperatures will likely impact plant phenology dramatically. The Canadian Arctic Archipelago is remote and difficult to reach, and there are few insights into the phenology of its plants. Data on current Arctic plant flowering times and how they vary across the Canadian Arctic Archipelago are needed to form a baseline to facilitate studies on the impact of climate change on Arctic plant phenology.

Methodology. We recorded the flowering times of 26 species from 12 families that are common to high-Arctic (lat. 81°N) and mid-Artic (lat. 63°N) locations in Nunavut, Canada, in 2013 and 2014. We compared differences in flowering times and flower abundance between the two locations and identified factors that might explain the differences.

Pivotal results. Species flowered at the same time or earlier and for a shorter duration at the high-Arctic location than at the mid-Arctic location. Different sublocales at a location explained more of the variation in flowering time than did mid- versus high-Arctic location or elevation. Peak flowering occurred one-third of the way through flowering. Plants at the mid-Arctic location produced more flowers per plant than did plants at the high-Arctic location. Relative order of species' flowering is consistent between the mid- and high-Arctic locations and between years.

Conclusions. Earlier flowering times of more northerly conspecifics are contrary to what might be expected given that temperatures are colder at the high-Arctic location than at the mid-Arctic location and that flowering time for a species is influenced by cumulative temperatures above a threshold. Our results suggest that plants at the northern location might be evolutionarily adapted to the shorter growing season and that plants have phenotypic plasticity across sublocales.

Keywords: arctic plants, Canadian Arctic Archipelago, duration of flowering, flower abundance, flowering time, Iqaluit, Lake Hazen, phenology.

Online enhancements: appendix figures and tables.

Introduction

The Canadian Arctic Archipelago is experiencing unprecedented climate change with temperatures rising twice as fast as the global average (Furgal and Prowse 2007; AMAP 2012; Stocker et al. 2013; Panchen and Gorelick 2015). Temperature influences the timing of flowering of many plant species (Rathcke and Lacey 1985). However, to measure the impact of climate change on flowering times of Arctic plants, the current timing of flowering (i.e., a baseline of Arctic plant phenology and how that phenology varies across this vast region) must be established. Changes in the timing of flowering and fruiting due to climate change have an impact on ecological communities, causing mismatches in the timing of flowering and pollinator arrival or emergence or in the timing of seed production and the departure of migratory birds that act as seed dispersers (Hegland et al. 2009; McKinney et al. 2012; Høye et al. 2013; Ellwood et al. 2014).

Temperature and photoperiod are key drivers in the mechanisms that control the timing of flowering (Rathcke and Lacey 1985). Plants first undergo a period of vernalization or a chilling period before flowering, a mechanism to prevent flowering during a warm period midwinter (Bernier and Périlleux 2005). Once the chilling requirements are met, a cumulative period of warm temperatures above a threshold temperature must be met before the plant initiates flowering (Rathcke and Lacey 1985; Bernier and Périlleux 2005; Kimball et al. 2014). Each species has different vernalization, cumulative temperature, and threshold temperature requirements. The threshold temperatures for Arctic

[1] Author for correspondence; e-mail: zoe.panchen@carleton.ca.

Manuscript received May 2016; revised manuscript received May 2016; electronically published August 31, 2016.

and alpine plants appear to range between −7° and 5°C (Kimball et al. 2014; Barrett et al. 2015). Initiation of flowering can also be triggered by a change in daylight hours (photoperiod; Bernier and Périlleux 2005). Some Arctic and alpine species are facultative photoperiodic with respect to flowering time, but temperature is the key driver in the initiation of flowering of Arctic and alpine plants, particularly at latitudes where there are 24 h of daylight per day for the entire growing season (lat. >63°N; Teeri 1976; Porsild and Cody 1980; Heide et al. 1990; Thórhallsdóttir 1998; Keller and Körner 2003; Heide 2005; Hülber et al. 2010). Arctic plants respond to warmer temperatures by flowering earlier (Wookey et al. 1993; Molau 1997; Stenström et al. 1997; Welker et al. 1997; Thórhallsdóttir 1998; Molau et al. 2005; Høye et al. 2007; Panchen and Gorelick 2015). However, the start, peak, and finish of flowering shift by different amounts (CaraDonna et al. 2014). Common garden experiments have shown that plants or seeds of a species from a more northerly latitude transplanted to a more southerly latitude flower earlier and for a shorter duration than conspecific plants from that more southerly latitude (Clausen et al. 1941; van Dijk et al. 1997; Weber and Schmid 1998; Olsson and Ågren 2002; Wagner and Simons 2009). The authors suggest that this might be due to evolutionary adaptation of the more northerly conspecifics to the harsher environment of a colder, shorter growing season.

We recorded the timing of flowering of plant species common to a high-Arctic location at Lake Hazen on northern Ellesmere Island, Nunavut, Canada, and a mid-Arctic location at Iqaluit on southern Baffin Island, Nunavut, in 2013 and 2014 to answer the following questions: (i) What are the timing and duration of flowering of Nunavut Arctic plants? (ii) What are the differences in timing and duration of flowering and flower abundance of conspecific plants between Lake Hazen and Iqaluit? (iii) What factors explain the differences in timing and duration of flowering? (iv) In relation to the duration of flowering, when do species peak flower?

Material and Methods

Locations

Flowering times of Arctic plant species were monitored at two locations in the Canadian Arctic Archipelago. The southern location was Iqaluit, Baffin Island, Nunavut, Canada (lat. 63°45′N, long. 68°33′W) and the northern location was Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut (lat. 81°49′N, long. 71°21′W; fig. 1). The range of elevations in our study was 4–109 m above sea level (a.s.l.) at Iqaluit and 161–784 m a.s.l. at Lake Hazen. There is no weather station at Lake Hazen; however, Eureka weather station (lat. 79.59°N, long. 85.56°W) is the closest weather station to Lake Hazen and experiences a climate similar to that of Lake Hazen (Soper and Powell 1985; Edlund and Alt 1989; Thompson 1994), and hence we used Eureka as a proxy to compare the climate between Iqaluit and Lake Hazen. Based on 30-yr mean temperatures (for 1981–2010), the growing season in Iqaluit is warmer than in Eureka, with the mean temperature during June–August 2.2°C warmer at Iqaluit than Eureka and 293.5 more annual growing degree days above zero at Iqaluit than Eureka, but both locations are typically snow free by mid-June (table 1). Monthly mean temperatures for June, July, and August in 2013 and 2014 were warmer in Iqaluit than Eureka. The summer of 2013 was colder than the summer of 2014 and had an average temperature below

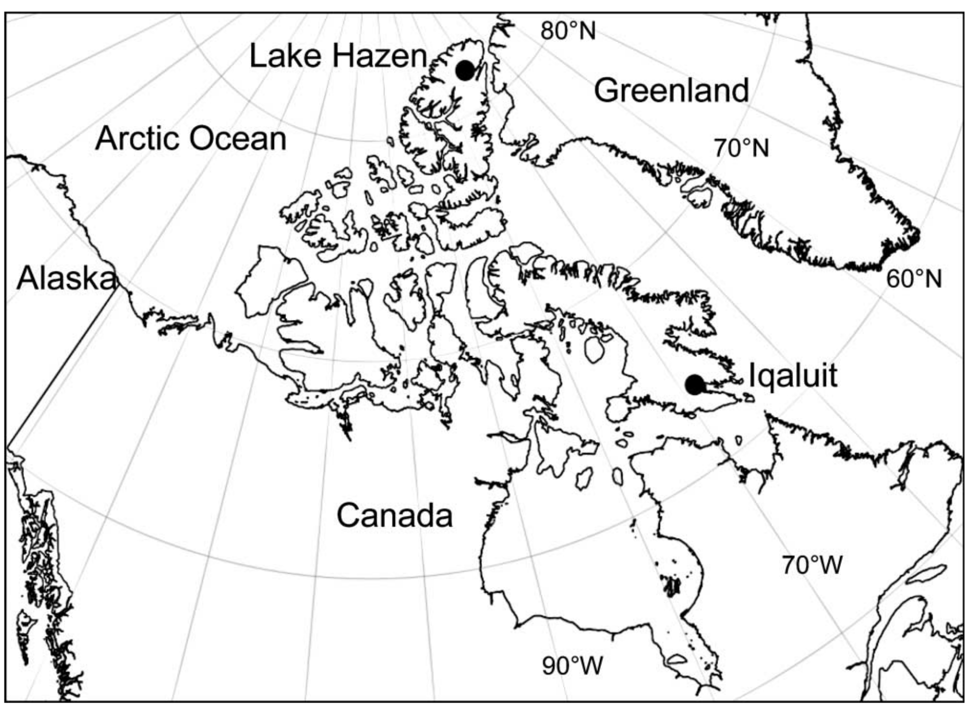

Fig. 1 Location of Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut (lat. 81°49′N, long. 71°21′W), and Iqaluit, Baffin Island, Nunavut, Canada (lat. 63°45′N, long. 68°33′W).

Table 1

Iqaluit and Eureka Environment Canada Weather Station Data

	30-yr mean		2013		2014	
	Iqaluit	Eureka	Iqaluit	Eureka	Iqaluit	Eureka
Mean temperature (°C):						
May	−4.4	−10.2	−6.7	−12.3	−1.7	−8.5
June	3.6	3.0	2.9	.5	4.4	1.0
July	8.2	6.1	7.2	4.5	9.1	5.9
August	7.1	3.2	7.6	−1.1	7.4	4.3
September	2.6	−6.4	2.3	−8.5	2.4	−4.6
June–August	6.3	4.1	5.9	1.3	6.9	3.7
Mean annual snowfall (cm)	229.3	60.3	...	...	...	...
No. June days with snow depth ≥1 cm	10.0	8.6	...	...	...	...
Annual degree days above 0°C	695.1	401.6	...	...	...	...

Note. Thirty-year (1981–2010), 2013, and 2014 mean temperatures (°C) for May to August and 30-yr mean annual snowfall, number of days in June with a snow depth ≥1 cm, and annual degree days above 0°C (Environment Canada 2016). The Eureka weather station is the closest weather station to Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, and experiences a similar climate (Edlund and Alt 1989; Thompson 1994).

the 30-yr mean temperature (for 1981–2010), whereas the average temperature for the summer of 2014 was similar to the 30-yr mean temperature at both Iqaluit and Eureka (table 1).

Both locations were divided into distinct sublocales: (1) at Iqaluit: Apex, Iqaluit City, Sylvia Grinnell Territorial Park, and the Road to Nowhere and (2) at Lake Hazen: Camp Hazen, Skeleton Lake, the plateau below and southeast of McGill Mountain, and the northeast upper slopes of McGill Mountain. Within each sublocale, areas with established populations of each species were selected before the start of flowering in 2013. Species were not always present at each sublocale; hence each species was monitored at one, two, or three sublocales (tables A1, A2, available online). The sublocales were within a 5-km radius of Iqaluit or the Lake Hazen park warden station.

Flowering Phenology Monitoring

Species common to Iqaluit and Lake Hazen (23 species in 2013 and 17 species in 2014) were monitored at Iqaluit from the last week in May to the third week of August and at Lake Hazen from the second week of June to the last week of July in 2013 and 2014 (tables A1, A2). A preliminary study was undertaken in 2013, wherein the date of start, peak, and finish of flowering of a species' population at a sublocale was recorded. The 2013 monitoring was qualitative and subjective, following an approach successfully used by Panchen et al. (2012). After reviewing the 2013 results, the approach in 2014 was changed to a quantitative approach wherein 30 plants of a species were randomly tagged at a sublocale and the number of flowers was counted on each tagged plant every site visit. The start, peak, and finish of flowering of the tagged plants were determined from the tagged plants' flower counts. The aim was to have 30 tagged flowering plants per species at each sublocale. We also aimed not to bias toward earlier-flowering plants by tagging plants before visible buds had appeared. However, in some cases, there were fewer than 30 plants at a sublocale or not all of the tagged plants flowered; hence the number of flowering tagged plants at a sublocale in 2014 was not always 30 (table A2). In both years, each sublocale at the two locations was visited twice per week (i.e., every 3–4 d). For both years, we defined start of flowering as the date on which open flowers were first observed, peak flowering as the date on which there were the greatest number of open flowers, finish of flowering as the date on which there were no more open flowers, and duration of flowering as the difference between the start and finish of flowering. Flowers were considered to be open when the petals were open (i.e., not in a bud), the petals looked fresh and were not wilted or discolored, the stigmas were visible and looked fresh, and the anthers were visible with pollen. The date was expressed as day of year (DOY; i.e., the number of days from the first of January 2013 or 2014). At Lake Hazen in 2013, we did not find *Arnica angustifolia* Vahl in time to record the start of flowering. At Lake Hazen in 2013, *Ranunculus hyperboreus* Rottb. and *Saxifraga cernua* L. had not reached peak flowering, and only 13 of the 23 species had finished flowering by the time we departed. At Lake Hazen in 2014, *Bistorta vivipara* (L.) Delarbre, *Saxifraga cespitosa* L., and *Saxifraga tricuspidata* Rottb. had not finished flowering by the time we departed. The inflorescence (capitulum holding many small flowers) of *A. angustifolia* was counted as a single flower. Less than five plants of the following species had second flowering, with only one or two flowers per plant, and therefore we excluded second flowering from the finish of flowering date: *Cardamine bellidifolia* L., *Cerastium arcticum* Lange, *S. cespitosa, Saxifraga oppositifolia* L., and *Silene acaulis* (L.) Jacq.

Temperature

In 2014, thermistor temperature sensors (TMC6-HD, Onset Computer, Bourne, MA) were installed 5 cm above the ground at each sublocale to measure temperatures at approximate plant height. Hourly temperature was recorded using HOBO H08-006-04 data loggers (Onset Computer) for the duration of the field season, but no sensor could be installed at the Iqaluit City sublocale.

Statistical Analysis

We used the Student's t difference of means test to analyze the difference between Iqaluit and Lake Hazen mean start of flowering DOY across species in 2013. The Student's t-test was repeated for peak and finish of flowering DOY and for duration of flowering separately across species. If the species was monitored at more than one sublocale in 2103, then the start, peak, or finish of flowering DOY used in the Student's t-test was the mean across the sublocales (i.e., the basic sampling unit was at the species level at the location).

We used Welch's difference of means test to analyze the difference between Iqaluit and Lake Hazen start of flowering DOY of tagged plants for each species separately in 2014. The Welch's test was repeated for peak and finish of flowering DOY and duration of flowering separately for each species in 2014. Each tagged plant was the basic sampling unit and the start, peak, and finish of flowering DOY of each tagged plant was a separate data point.

We used separate linear mixed-effects models for each start, peak, and finish of flowering DOY and duration of flowering in 2014 to determine how much of the start, peak, finish, or duration of flowering time variation was explained by location (Lake Hazen vs. Iqaluit), elevation, and sublocale (nested within location, because sublocales are unique to each location). The mixed-effects model used restricted maximum likelihood methods where species was a random effect; location, elevation, and sublocale were fixed effects; and each tagged plant was the basic sampling unit.

To determine when peak flowering occurred in relation to duration of flowering, we calculated the mean percentage time to peak flowering for each species at Lake Hazen and Iqaluit separately in 2014. That is, we computed the ratio of number of days from start to peak flowering in relation to number of days from start to finish of flowering and expressed this as a percentage. We also used Welch's difference of means test to analyze the difference in peak flower count between Lake Hazen and Iqaluit in 2014 for each species. *Bistorta vivipara, S. cespitosa*, and *S. tricuspidata* were not included in the 2014 analysis of finish and duration of flowering, percentage time to peak flowering, and peak flower count, because not all tagged plants had finished flowering. We also excluded *Alopecurus magellanicus* Lam., *Arctagrostis latifolia* (R.Br.) Griseb., and *Eriophorum scheuchzeri* Hoppe from the percentage time to peak flowering and peak flower count analysis, because we counted the panicle as a single flower for these species, and there was always only one panicle per plant at both Lake Hazen and Iqaluit.

To determine whether the order of flowering across species was consistent between Lake Hazen and Iqaluit, we correlated the date of species' mean peak flowering DOY at Lake Hazen versus Iqaluit in 2013 and 2014 separately and ran a Spearman's rank correlation (ρ) for each. Similarly, to determine whether the order of flowering was consistent between years, we correlated the date of species' peak flowering DOY in 2013 versus 2014 at Lake Hazen and Iqaluit separately and ran Spearman's rank correlations for each. All statistical analysis was conducted using JMP11 (SAS Institute, Cary, NC).

Results

In 2013, on average across species, duration of flowering was significantly longer at more southern Iqaluit than at more northern Lake Hazen ($t = 2.06$, $P = 0.038$, $n = 13$, 6 d longer at Iqaluit); flowering started significantly earlier at Iqaluit than at Lake Hazen ($t = 2.02$, $P = 0.039$, $n = 22$, 8 d earlier at Iqaluit), but there was no significant difference in the timing of peak or finish of flowering DOY at the two locations (peak flowering: $t = 2.02$, $P = 0.319$, $n = 21$; finish of flowering: $t = 2.06$, $P = 0.918$, $n = 13$; fig. 2). In 2014, on average, most species flowered for a significantly longer duration at Iqaluit than at Lake Hazen; most species started, peaked, and finished flowering significantly earlier at more northern Lake Hazen than at more southern Iqaluit (table 2).

More than 77% of start, peak, or finish of flowering and 39% of duration of flowering was explained by location, elevation, sublocale, and species (table 3). Sublocale at a location explained significantly more of the variation in time and duration of flowering in 2014 than did the location (Lake Hazen vs. Iqaluit) or elevation (table 3). Although their influence was still less than that of sublocale, location and elevation had a greater influence on finish of flowering than did start, peak, or duration of flowering (table 3).

Peak flowering occurred approximately one-third of the way through flowering duration (table 4). There were significantly higher flower counts of species at more southern Iqaluit than of species at more northern Lake Hazen ($t = 4.67$, $P < 0.0001$, $n = 318$ at Lake Hazen and 553 at Iqaluit).

The order of species' peak flowering was consistent between Lake Hazen and Iqaluit (2013: $R^2 = 0.42$, $\rho = 0.64$, $P < 0.002$, $n = 21$; 2014: $R^2 = 0.70$, $\rho = 0.84$, $P < 0.0001$, $n = 17$; figs. 3, A1; figs. A1, A2 available online) and between years (Lake Hazen: $R^2 = 0.84$, $\rho = 0.92$, $P < 0.0001$, $n = 13$; Iqaluit: $R^2 = 0.76$, $\rho = 0.84$, $P < 0.0005$, $n = 13$). The start and finish of flowering were also consistent between Lake Hazen and Iqaluit in 2014 (start of flowering: $R^2 = 0.80$, $\rho = 0.85$, $P < 0.0001$, $n = 17$; finish of flowering: $R^2 = 0.52$, $\rho = 0.71$, $P < 0.005$, $n = 14$; fig. A2) but less so for start of flowering in 2013 ($R^2 = 0.37$, $\rho = 0.55$, $P < 0.008$, $n = 22$) and not at all for finish of flowering in 2013 ($R^2 = 0.20$, $\rho = 0.35$, $P > 0.1$, $n = 13$).

Mean temperature at 5 cm aboveground across sublocales was 11.1°C at Lake Hazen and 11.3°C at Iqaluit (June 18 to July 28, 2014). However, diurnal temperatures varied more at more southern Iqaluit than at more northern Lake Hazen, with temperatures rising higher during the day but dipping lower at night (table 5). Average temperatures at 5 cm aboveground differed among sublocales at Iqaluit and Lake Hazen (table 5). At Lake Hazen, the midelevation sublocale (451 m a.s.l.) was, as expected, warmer than the high-elevation sublocale (781 m a.s.l.) but also warmer than sublocales at lower elevations (161 and 287 m a.s.l.) because of the cooling effect of the frozen lake on low-elevation sublocales close to the lake. Similarly, at Iqaluit, Sylvia Grinnell Park sublocale (50 m a.s.l.) was colder than the other two sublocales (33 and 105 m a.s.l.) because of its proximity to a frozen river and the ice-covered ocean.

Discussion

With dramatic climate change occurring in the Arctic, our study aimed to establish a baseline of Nunavut flowering times and how and why plant flowering times varied between a high-Arctic (Lake Hazen) and mid-Arctic (Iqaluit) location. Plants at our northern location, Lake Hazen, tended to flower earlier and for a shorter period of time than conspecific plants at our

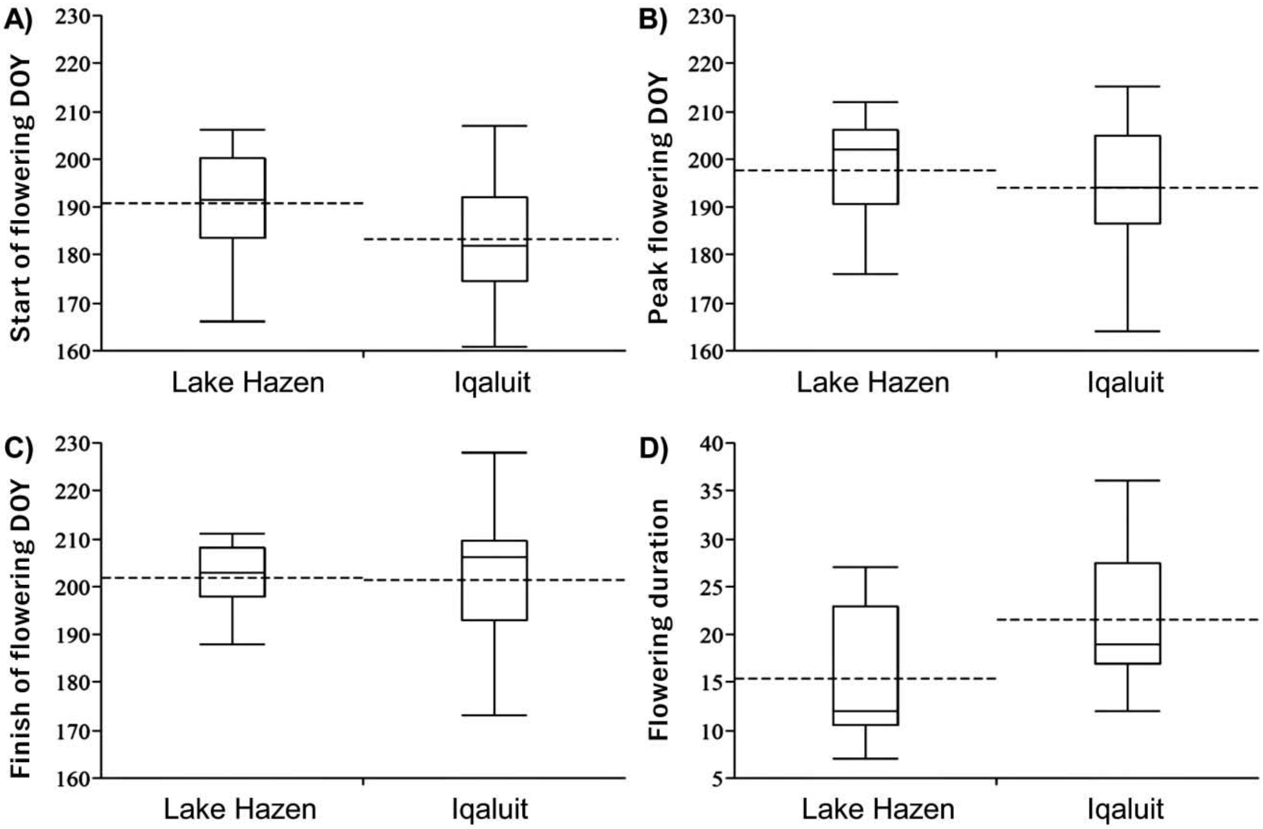

Fig. 2 Comparison of mean start, peak, and finish of flowering day of year (DOY) and duration of flowering across species at Lake Hazen, Ellesmere Island, Nunavut, versus Iqaluit, Baffin Island, Nunavut, in 2013. *A*, Flowering started significantly earlier at Iqaluit than at Lake Hazen ($t = 2.02$, $P = 0.039$, $n = 22$, 8 d earlier at Iqaluit). *B*, Flowering peaked at the same time at Iqaluit and Lake Hazen ($t = 2.02$, $P = 0.319$, $n = 21$). *C*, Flowering finished at the same time at Iqaluit and Lake Hazen ($t = 2.06$, $P = 0.918$, $n = 13$). *D*, Flowering duration was significantly longer at Iqaluit than at Lake Hazen ($t = 2.06$, $P = 0.038$, $n = 13$, 6 d longer at Iqaluit). The box plots show the quartiles and mean (dotted line) flowering DOY and flowering duration.

southern location, Iqaluit. We had expected the opposite given that temperatures are warmer at Iqaluit than at Lake Hazen, with a greater number of growing degree days (table 1) and higher daily maximum temperatures at Iqaluit (table 5), and given that plants require a certain number of growing degree days above a threshold temperature before they initiate flowering (Kimball et al. 2014). In 2014, plants at Lake Hazen, in general, started, peaked, and finished flowering earlier and flowered for a shorter duration than did plants at Iqaluit. However, in 2013, which had a particularly cold, short growing season, plants at Lake Hazen, although they started flowering later than those at Iqaluit, had caught up with plants at Iqaluit by peak flowering time. Growing degree days required for flowering to start accumulate above a temperature threshold (Kimball et al. 2014) and hence, with the particularly cold year, possibly resulted in the later start of flowering at Lake Hazen in 2013. Once temperatures start rising above the temperature threshold, plants farther north appear to require fewer growing degree days and complete their reproductive cycle earlier and/or quicker. The lack of statistical difference for finish of flowering across species in 2013 between Lake Hazen and Iqaluit could be because only the earlier flowering species could be compared (13 of 23 species).

Our findings concur with common garden experiments and long-term studies showing earlier and shorter duration of flowering of plants from farther north, where we hypothesize the phenological difference in conspecifics is potentially due to evolutionary adaptation along a latitudinal gradient (van Dijk et al. 1997; Weber and Schmid 1998; Olsson and Ågren 2002; Wagner and Simons 2009; Rossi 2015; Roy et al. 2015). Our approach, however, was different in that the conspecific plants that we studied were left growing in situ, whereas the common garden experiments moved the conspecific plants and seeds to be studied to a common location (Larl and Wagner 2006). The hypothesis that there is phenological evolutionary adaptation of conspecifics along a latitudinal gradient requires additional study, and in our study, comparison of only two latitudes was also a limiting factor. Snowmelt out date could also be a contributing factor in the difference in time of flowering between Iqaluit and Lake Hazen. Several studies of Arctic plants have shown that time of flowering is dependent on snowmelt out date (Eriksen et al. 1993; Woodley and Svoboda 1994; Molau 1997; Stenström et al. 1997; Aerts et al. 2006; Larl and Wagner 2006; Iler et al. 2013; Bjorkman et al. 2015), but other Arctic studies, particularly those conducted where snow accumulation is low, did not find a relationship between time of flowering and snowmelt

Table 2

Difference of Mean Flowering of Lake Hazen, Ellesmere Island, Nunavut, Tagged Plants versus Their Conspecific Tagged Plants at Iqaluit, Baffin Island, Nunavut

	Difference of mean flowering			
Species (family)	Start	Peak	Finish	Duration
Alopecurus magellanicus (Poaceae)	−2.78***	−2.78***	−4.43***	−4.43*
Arctagrostis latifolia (Poaceae)	−8.03***	−8.03***	−9.05***	−9.05
Arnica angustifolia (Asteraceae)	2.62*	.38	−2.61*	−2.61***
Bistorta vivipara (Polygonaceae)	−1.11	−5.12**	...	...
Cardamine bellidifolia (Brassicaceae)	−5.53*	−8.24*	−10.93*	−10.93
Cassiope tetragona (Ericaceae)	4.64**	5.58***	4.14**	4.14
Cerastium arcticum (Caryophyllaceae)	−5.81***	−6.31**	−3.87*	−3.87
Chamerion latifolium (Onagraceae)	−11.54***	−18.00***	−25.83***	−25.83***
Dryas integrifolia (Rosaceae)	−5.95***	−10.87***	−17.14***	−17.14***
Eriophorum scheuchzeri (Cyperaceae)	4.00***	2.50***	−11.97***	−11.97***
Eutrema edwardsii (Brassicaceae)	8.86***	7.93***	5.87***	5.87***
Pedicularis hirsuta (Orobanchaceae)	−3.51*	−4.53**	−10.26***	−10.26***
Saxifraga cespitosa (Saxifragaceae)	−.61	2.48	...	...
Saxifraga oppositifolia (Saxifragaceae)	3.70*	4.87**	5.86***	5.86*
Saxifraga tricuspidata (Saxifragaceae)	−3.55**	−6.26***	...	...
Silene acaulis (Caryophyllaceae)	−2.40*	−5.59***	−2.29	−2.29
Silene uralensis (Caryophyllaceae)	−13.67***	−12.74***	−11.10***	−11.10
All species	−3.73***	−4.60***	−9.58***	−8.75***

Note. Difference in mean start, peak, finish, and duration of flowering in 2014 of Lake Hazen, Ellesmere Island, Nunavut, tagged plants versus their conspecific tagged plants at Iqaluit, Baffin Island, Nunavut. A positive value indicates that the Iqaluit species flowered earlier or for a shorter duration, and a negative value indicates that the Lake Hazen species flowered earlier or for a shorter duration.

* $P < 0.05$.

** $P < 0.001$.

*** $P < 0.0001$.

out date (Thórhallsdóttir 1998; Molau et al. 2005; Ellebjerg et al. 2008; Bienau et al. 2015). Although mean annual snowfall (1981–2010) is greater at Iqaluit than at Eureka, the number of days in June with snow accumulation is only 1.4 d different (table 1), and hence it seems unlikely that the difference in flowering times between Lake Hazen and Iqaluit is due to differences in snowmelt out date. Photoperiod could also be a contributing factor to earlier flowering at Lake Hazen than at Iqaluit. However, both locations experience 24 h of daylight per day at least 1 mo before the earliest plants start to flower, and hence photoperiod also seems unlikely to be a contributing factor to the difference in flowering time.

Although there is a significant difference in the time of flowering between Lake Hazen and Iqaluit, the mean difference in peak flowering across 17 common Arctic plant species in 2014 was just 5 d, which is biologically quite small given the 18° of latitude difference between Lake Hazen and Iqaluit. Chmielewski and Rötzer (2001) calculated leafing out in Europe progressed north by 44 km/d or approximately 2.5 d later per degree of latitude, which suggests that there should be a much greater difference in phenology across latitudes than we observed. Isotherms in the Canadian Arctic, however, are widely spaced in the summer months (i.e., there is less latitudinal difference in temperature in summer months than in winter months; Przybylak 2003). Our own temperature data showed only a small difference in temperatures between Lake Hazen and Iqaluit, and the difference in the June–August 30-yr mean temperature between Iqaluit and Eureka was 2.2°C. Since timing of flowering is often dependent on temperature in the month or months prior to flowering (Fitter et al. 1995; Panchen et al. 2012; Panchen and

Table 3

Linear Mixed-Effects Model Results of the Variation in the 2014 Start, Peak, Finish, or Duration of Flowering of Tagged Plants at Lake Hazen, Ellesmere Island, Nunavut, versus Iqaluit, Baffin Island, Nunavut

	Overall model			Location			Elevation			Sublocale		
	R^2	P	n	F	df	P	F	df	P	F	df	P
Start of flowering	.77	<.0001	1380	4.10	1	.043	3.51	1	.061	32.85	6	<.0001
Peak flowering	.78	<.0001	1380	.55	1	.458	.05	1	.827	26.38	6	<.0001
Finish of flowering	.78	<.0001	1116	12.85	1	.0004	7.52	1	.006	15.95	6	<.0001
Duration of flowering	.39	<.0001	1116	.11	1	.735	.23	1	.630	4.75	6	<.0001

Note. Linear mixed-effects model results with species as a random effect showing that most of the variation in the 2014 start, peak, or finish of flowering DOY or duration of flowering of tagged plants was explained by sublocale and that very little was explained by elevation and location (Lake Hazen, Ellesmere Island, Nunavut, vs. Iqaluit, Baffin Island, Nunavut). df = degrees of freedom; n = number of tagged plants.

Table 4

Percentage Time to Peak Flowering in 2014 of Tagged Plants' Mean Peak Flowering Time at Lake Hazen, Ellesmere Island, Nunavut, and Iqaluit, Baffin Island, Nunavut

	Lake Hazen			Iqaluit		
Species	Mean (%)	*n*	SD	Mean (%)	*n*	SD
Arnica angustifolia	48.9	19	3.9	46.3	56	10.8
Cardamine bellidifolia	30.8	12	16.9	31.6	26	34.9
Cassiope tetragona	27.1	41	15.3	27.5	30	15.1
Cerastium arcticum	32.4	22	19.5	35.3	54	21.4
Chamerion latifolium	12.6	19	19.8	37.0	58	16.3
Dryas integrifolia	18.9	21	20.2	32.7	58	18.7
Eutrema edwardsii	28.5	41	22.9	31.6	59	17.5
Pedicularis hirsuta	19.8	16	27.1	18.9	58	18.5
Saxifraga oppositifolia	36.1	60	13.7	31.8	38	22.9
Silene acaulis	20.9	30	10.5	37.3	59	16.2
Silene uralensis	27.0	29	15.2	22.3	56	18.9
All species	28.5	310	18.9	32.3	552	20.2

Note. n = number of tagged plants; SD = standard deviation.

Gorelick 2015), this small difference in temperature across latitudes may explain the small difference in time of flowering between greatly differing latitudes. It is also interesting to note that latitude and elevation are not major factors in time of flowering (Ge et al. 2014), and yet there was a consistent order of flowering between species in Iqaluit versus Lake Hazen and between 2013 and 2014 at both locations, indicating that relative timing of flowering in a season is species specific. Although it is often assumed that temperatures are colder at higher elevations, this is not the case at Lake Hazen and Iqaluit, where proximity

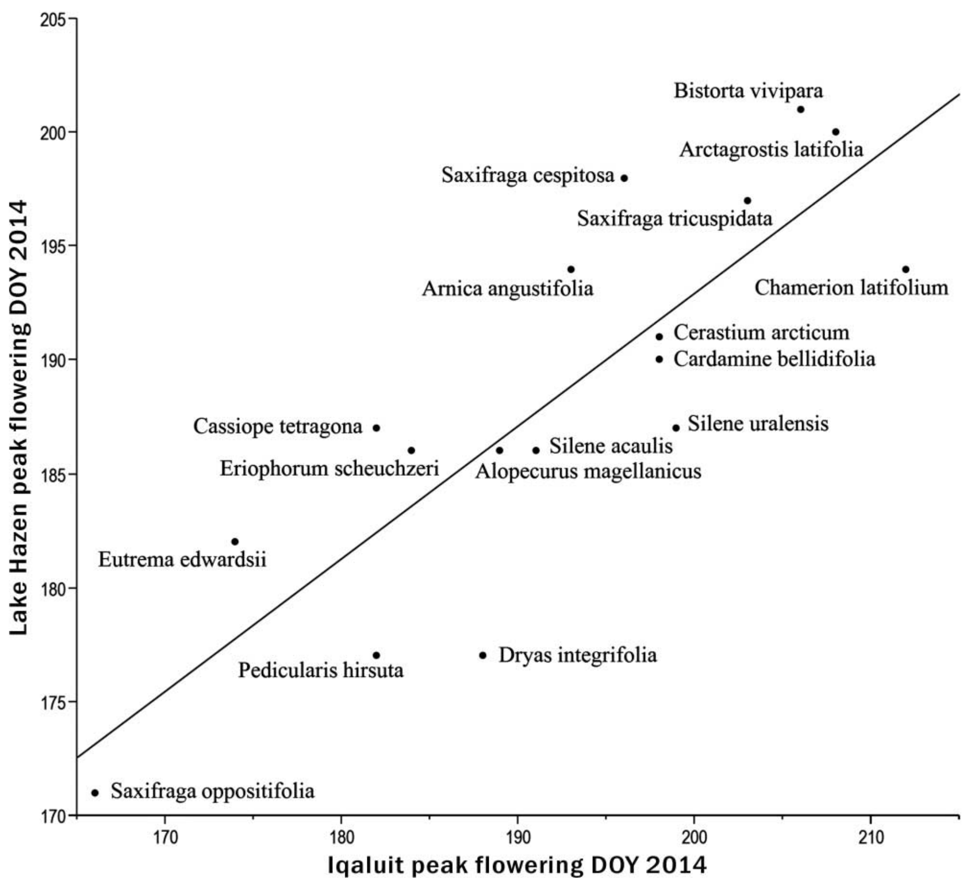

Fig. 3 Comparison of order of peak flowering day of year (DOY) by species in 2014 at Lake Hazen, Ellesmere Island, Nunavut, and Iqaluit, Baffin Island, Nunavut, showing that the order of peak flowering is consistent between Iqaluit and Lake Hazen (R^2 = 0.70, ρ = 0.84, $P < 0.0001$, n = 17).

Table 5

Mean Daily Maximum, Minimum, and Mean Temperatures 5 cm aboveground at Sublocales at Lake Hazen, Ellesmere Island, Nunavut, and Iqaluit, Baffin Island, Nunavut, June 18–July 27, 2014

		Temperature		
	Elevation (m)	Mean (°C)	Maximum (°C)	Minimum (°C)
Lake Hazen sublocale:				
Camp Hazen	161	11.3	16.2	6.6
Skeleton Lake	287	11.2	16.5	4.6
McGill Mountain plateau	451	12.6	19.9	5.3
McGill Mountain upper slopes	784	9.4	14.3	5.5
Iqaluit sublocale:				
Apex	33	11.7	22.7	4.2
Sylvia Grinnell	50	10.5	21.1	2.5
Road to Nowhere	105	11.6	19.0	7.5

to frozen bodies of water can also influence the temperature; this is hence why elevation may not have been a strong contributing factor to flowering time in our study. Phenological records, such as herbarium specimens, which could be used to assess plant flowering responses to climate change, have been sparsely collected across the Arctic, potentially necessitating a comparison across the region rather than a localized comparison, as has typically been done in temperate studies (Primack et al. 2004; Panchen et al. 2012). Indications of the small variation across the region in time of flowering in a particular year may aid in Arctic plant phenology–climate change studies (Lavoie and Lachance 2006; Calinger et al. 2013; Davis et al. 2015).

Our results show that there is greater variation in the timing of flowering between sublocales at a location (Lake Hazen vs. Iqaluit) than between those two distant locations, possibly suggesting phenotypic plasticity of plants between sublocales and evolutionary adaptation at different distant locations (Roy et al. 2015). Our temperature measurements at plant height support this finding in that there was greater variation in temperature between sublocales at a location than between locations. The combination of Arctic plant phenological responses to varying climates suggests that, with climate change, Arctic plants have the potential to respond to climate change through phenotypic plasticity in the short term and by evolutionary adaptation in the long term (Larl and Wagner 2006; Crawford et al. 2009; Anderson et al. 2012; Roy et al. 2015).

The peak of Arctic plant flowering is skewed toward the start of flowering, with most species reaching peak flowering approximately one-third through the flowering duration, which is consistent with the findings of Eriksen et al. (1993), Alatalo and Totland (1997), and Molau (1997). This is expected in an environment with a short growing season where, when optimal flowering conditions are reached, flowering must proceed rapidly to maximize reproductive success. The significantly higher flower abundance at Iqaluit than at Lake Hazen is also what might be expected given the harsher environment at Lake Hazen, and it also suggests the potential for greater reproductive success at a southern location than at a northern location. The higher flower abundance at Iqaluit than at Lake Hazen could also potentially be a factor in the longer flowering duration at Iqaluit than at Lake Hazen.

In summary, our results show that the timing of flowering of Arctic species in the Canadian Arctic Archipelago can be earlier farther north and is explained more by sublocales than by latitude or elevation. Given that our findings are in some ways contrary to what might be expected, they should be taken into consideration when modeling and predicting impacts of climate change on the Arctic ecosystem.

Acknowledgments

We thank the Hamlets and Hunter and Trapper Organizations of Grise Fiord, Resolute Bay, and Iqaluit for their support of the research; field assistants Sofia Jain-Schlaepfer, Joan Makaroff, Emma Micalizzi, Orla Osborne, and Teresa Tufts; Paul Smith at the National Wildlife Research Centre for loaning the temperature data loggers; and two anonymous reviewers for their insightful comments and suggestions. This research was funded by a Natural Sciences and Engineering Research Council (NSERC) of Canada Canadian Graduate Scholarship, Northern Scientific Training Program travel bursaries, and Canadian Federation of University Women Beverley Jackson Fellowship to Zoe A. Panchen; an NSERC Discovery Grant to Root Gorelick; and in-kind support from Parks Canada's Nunavut Field Unit. This research was conducted under Nunavut Department of Environment wildlife research permits WL 2013-039 and WL 2014-021, Nunavut Territorial Parks park use permits 2013-01 PU and 2014-02 PU, and Parks Canada research and collections permits QUT 2013-13959 and QUT-2014-16198.

Literature Cited

Aerts R, JHC Cornelissen, E Dorrepaal 2006 Plant performance in a warmer world: general responses of plants from cold, northern biomes and the importance of winter and spring events. Plant Ecol 182:65–77.

Alatalo JM, O Totland 1997 Response to simulated climatic change in an alpine and subarctic pollen-risk strategist, *Silene acaulis*. Global Change Biol 3:74–79.

AMAP (Arctic Monitoring and Assessment Programme) 2012 Climate change in the Arctic: a hot topic. SWIPA 2011: snow, water, ice and permafrost in the Arctic. AMAP, Oslo, Norway.

Anderson JT, DW Inouye, AM McKinney, RI Colautti, T Mitchell-Olds 2012 Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proc R Soc B 279:3843–3852.

Barrett RTS, RD Hollister, SF Oberbauer, CE Tweedie 2015 Arctic plant responses to changing abiotic factors in northern Alaska. Am J Bot 102:2020–2031.

Bernier G, C Périlleux 2005 A physiological overview of the genetics of flowering time control. Plant Biotechnol J 3:3–16.

Bienau MJ, M Kröncke, WL Eiserhardt, A Otte, BJ Graae, D Hagen, A Milbau, W Durka, RL Eckstein 2015 Synchronous flowering despite differences in snowmelt timing among habitats of *Empetrum hermaphroditum*. Acta Oecol 69:129–136.

Bjorkman AD, SC Elmendorf, AL Beamish, M Vellend, GHR Henry 2015 Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. Global Change Biol 21:4651–4661.

Calinger KM, S Queenborough, PS Curtis 2013 Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America. Ecol Lett 16:1037–1044.

CaraDonna PJ, AM Iler, DW Inouye 2014 Shifts in flowering phenology reshape a subalpine plant community. Proc Natl Acad Sci USA 111:4916–4921.

Chmielewski F-M, T Rötzer 2001 Response of tree phenology to climate change across Europe. Agric For Meteorol 108:101–112.

Clausen J, DD Keck, WM Hiesey 1941 Regional differentiation in plant species. Am Nat 75:231–250.

Crawford RMM, HM Chapman, LC Smith 2009 Adaptation to variation in growing season length in Arctic populations of *Saxifraga oppositifolia* L. Bot J Scotl 47:177–192.

Davis CC, CG Willis, B Connolly, C Kelly, AM Ellison 2015 Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms. Am J Bot 102:1599–1609.

Edlund SA, BT Alt 1989 Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada. Arctic 42:3–23.

Ellebjerg SM, MP Tamstorf, L Illeris, A Michelsen, BU Hansen 2008 Inter-annual variability and controls of plant phenology and productivity at Zackenberg. Adv Ecol Res 40:249–273.

Ellwood E, S Playfair, C Polgar, R Primack 2014 Cranberry flowering times and climate change in southern Massachusetts. Int J Biometeorol 58:1693–1697.

Environment Canada 2016 National climate data and information archive. http://www.ncdc.noaa.gov/.

Eriksen B, U Molau, M Svensson 1993 Reproductive strategies in two Arctic *Pedicularis* species (Scrophulariaceae). Ecography 16:154–166.

Fitter AH, RSR Fitter, ITB Harris, MH Williamson 1995 Relationships between first flowering date and temperature in the flora of a locality in central England. Funct Ecol 9:55–60.

Furgal C, TD Prowse 2007 Northern Canada. Pages 57–118 *in* DS Lemmen, FJ Warren, J Lacroix, eds. From impacts to adaptation: Canada in a changing climate. Natural Resources Canada, Ottawa.

Ge Q, H Wang, T Rutishauser, J Dai 2014 Phenological response to climate change in China: a meta-analysis. Global Change Biol 21:265–274.

Hegland SJ, A Nielsen, A Lázaro, A-L Bjerknes, Ø Totland 2009 How does climate warming affect plant-pollinator interactions? Ecol Lett 12:184–195.

Heide OM 2005 Ecotypic variation among European Arctic and alpine populations of *Oxyria digyna*. Arct Antarct Alp Res 37:233–238.

Heide OM, K Pedersen, E Dahl 1990 Environmental control of flowering and morphology in the high-arctic *Cerastium regelii*, and the taxonomic status of *C. jenisejense*. Nord J Bot 10:141–147.

Høye TT, E Post, H Meltofte, NM Schmidt, MC Forchhammer 2007 Rapid advancement of spring in the high Arctic. Curr Biol 17: R449–R451.

Høye TT, E Post, NM Schmidt, K Trøjelsgaard, MC Forchhammer 2013 Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. Nat Clim Change 3:759–763.

Hülber K, M Winkler, G Grabherr 2010 Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species. Funct Ecol 24:245–252.

Iler AM, TT Hoye, DW Inouye, NM Schmidt 2013 Nonlinear flowering responses to climate: are species approaching their limits of phenological change? Philos Trans R Soc B 368:20120489.

Keller F, C Körner 2003 The role of photoperiodism in alpine plant development. Arct Antarct Alp Res 35:361–368.

Kimball KD, ML Davis, DM Weihrauch, GLD Murray, K Rancourt 2014 Limited alpine climatic warming and modeled phenology advancement for three alpine species in the northeast United States. Am J Bot 101:1437–1446.

Larl I, J Wagner 2006 Timing of reproductive and vegetative development in *Saxifraga oppositifolia* in an alpine and a subnival climate. Plant Biol 8:155–166.

Lavoie C, D Lachance 2006 A new herbarium-based method for reconstructing the phenology of plant species across large areas. Am J Bot 93:512–516.

McKinney AM, PJ CaraDonna, DW Inouye, WA Barr, CD Bertelsen, NM Waser 2012 Asynchronous changes in phenology of migrating broad-tailed hummingbirds and their early-season nectar resources. Ecology 93:1987–1993.

Molau U 1997 Responses to natural climatic variation and experimental warming in two tundra plant species with contrasting life forms: *Cassiope tetragona* and *Ranunculus nivalis*. Global Change Biol 3:97–107.

Molau U, U Nordenhäll, B Eriksen 2005 Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. Am J Bot 92:422–431.

Olsson K, J Ågren 2002 Latitudinal population differentiation in phenology, life history and flower morphology in the perennial herb *Lythrum salicaria*. J Evol Biol 15:983–996.

Panchen ZA, R Gorelick 2015 Flowering and fruiting responses to climate change of two Arctic plant species, purple saxifrage (*Saxifraga oppositifolia*) and mountain avens (*Dryas integrifolia*). Arctic Sci 1: 45–58.

Panchen ZA, RB Primack, T Aniśko, RE Lyons 2012 Herbarium specimens, photographs, and field observations show Philadelphia area plants are responding to climate change. Am J Bot 99:751–756.

Porsild AE, WJ Cody 1980 Vascular plants of continental Northwest Territories, Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa.

Primack D, C Imbres, RB Primack, AJ Miller-Rushing, P Del Tredici 2004 Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. Am J Bot 91:1260–1264.

Przybylak R 2003 The climate of the Arctic. Kluwer, Boston.

Rathcke B, EP Lacey 1985 Phenological patterns of terrestrial plants. Annu Rev Ecol Syst 16:179–214.

Rossi S 2015 Local adaptations and climate change: converging sensitivity of bud break in black spruce provenances. Int J Biometeorol 59:827–835.

Roy DB, TH Oliver, MS Botham, B Beckmann, T Brereton, RLH Dennis, C Harrower, AB Phillimore, JA Thomas 2015 Similarities in butterfly emergence dates among populations suggest local adaptation to climate. Global Change Biol 21:3313–3322.

Stenström M, F Gugerli, GHR Henry 1997 Response of *Saxifraga oppositifolia* L. to simulated climate change at three contrasting latitudes. Global Change Biol 3:44–54.

Stocker TF, D Qin, G-K Plattner, LV Alexander, SK Allen, NL Bindoff, F-M Bréon, et al 2013 technical summary. Pages 33–115 *in* TF Stocker, D Qin, G-K Plattner, M Tignor, SK Allen, J Boschung, A Nauels, Y Xia, V Bex, PM Midgley, eds. Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York.

Teeri JA 1976 Phytotron analysis of a photoperiodic response in a high Arctic plant species. Ecology 57:374–379.

Thompson W 1994 Climate. Pages 1–78 *in* Parks Canada, ed. Resource description and analysis: Ellesmere Island, National Park Reserve. National Resource Conservation Section, Prairie and Northern Region, Parks Canada, Department of Canadian Heritage, Winnipeg, Manitoba, Canada.

Thórhallsdóttir TE 1998 Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. Oecologia 114:43–49.

van Dijk H, P Boudry, H McCombre, P Vernet 1997 Flowering time in wild beet (*Beta vulgaris* ssp. *maritima*) along a latitudinal cline. Acta Oecol 18:47–60.

Wagner I, AM Simons 2009 Divergence among Arctic and alpine populations of the annual, *Koenigia islandica*: morphology, life-history, and phenology. Ecography 32:114–122.

Weber E, B Schmid 1998 Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. Am J Bot 85:1110–1121.

Welker JM, U Molau, AN Parsons, CH Robinson, PA Wookey 1997 Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. Global Change Biol 3:61–73.

Woodley EJ, J Svoboda 1994 Effects of habitat on variation of phenology and nutrient concentration among four common plant species of the Alexandria Fiord lowland. Pages 157–175 *in* J Svoboda, B Freedman, eds. Ecology of a polar oasis: Alexandria Fiord, Ellesmere Island, Canada. Captus, Toronto.

Wookey PA, AN Parsons, JM Welker, JA Potter, TV Callaghan, JA Lee, MC Press 1993 Comparative responses of phenology and reproductive development to simulated environmental change in sub-Arctic and high Arctic plants. Oikos 67:490–502.