NRC Research Press

ARTICLE

Flowering and fruiting responses to climate change of two Arctic plant species, purple saxifrage (*Saxifraga oppositifolia*) and mountain avens (*Dryas integrifolia*)

Zoe A. Panchen and Root Gorelick

Abstract: In temperate regions, there are clear indications that spring flowering plants are flowering earlier due to rising temperatures of contemporary climate change. Temperatures in temperate regions are rising predominantly in spring. However, Arctic regions are seeing unprecedented temperature increases, predominantly towards the end of the growing season. We might, therefore, expect to see earlier flowering of later-season flowering Arctic plants. Parks Canada has been monitoring purple saxifrage (*Saxifraga oppositifolia*) and mountain avens (*Dryas integrifolia*) flowering and fruiting times for 20 years at Tanquary Fiord, Quttinirpaaq National Park, Ellesmere Island. *Saxifraga oppositifolia* flowers in early spring, while *D. integrifolia* flowers in midsummer. Over the 20-year period, Tanquary Fiord's annual and late-summer temperatures have risen significantly. During the same timeframe, *D. integrifolia* showed a trend towards earlier flowering and fruiting, but *S. oppositifolia* showed no changes in flowering or fruiting time. Flowering time was related to monthly temperatures just prior to flowering. The number of flowers produced was related to the previous autumn's monthly temperatures. We found no relationship between flowering time and snowmelt date. Our findings suggest that Arctic community level ecological effects from climate change induced phenology changes will differ from those in temperate regions.

Key words: climate change, mountain avens, purple saxifrage, ITEX, phenology.

Résumé : Dans les régions tempérées, il y a des signes clairs que les plantes à floraison printanière fleurissent plus tôt en raison des températures à la hausse attribuable au changement climatique contemporain. Les températures dans les régions tempérées augmentent principalement au printemps. Cependant, dans les régions arctiques, on constate des augmentations de température sans précédent, principalement vers la fin de la période de croissance. Nous pourrions, donc, nous attendre à voir une floraison plus tôt des plantes arctiques à floraison plus tardive. Depuis 20 ans, Parc Canada suit de près les périodes de floraison et de fructification de la saxifrage à feuilles opposées (*Saxifraga oppositifolia*) et de la dryade à feuilles entières (*Dryas integrifolia*) au Fjord Tanquary, Parc national du Quttinirpaaq, l'île d'Ellesmere. *Saxifraga oppositifolia* fleurit tôt au printemps, tandis que *D. integrifolia* fleurit au milieu de l'été. Au cours de la période de 20 ans, les températures annuelles et de la fin d'été au Fjord Tanquary ont augmenté considérablement. Pendant la même période, *D. integrifolia* a manifesté une tendance vers une floraison et une fructification plus précoce, tandis qu'il n'y a pas eu de changement noté dans le temps de floraison et de fructification de *S. oppositifolia*. Le temps de floraison était lié aux températures mensuelles justes avant la floraison. Le nombre de fleurs produites était lié aux températures mensuelles de l'automne

Received 20 April 2015. Accepted 1 October 2015.

Z.A. Panchen and R. Gorelick. Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada
Corresponding author: Zoe A. Panchen (e-mail: Zoe.Panchen@Carleton.ca).

Arctic Science **1**: 45–58 (2015) dx.doi.org/10.1139/as-2015-0016

précédent. Nous n'avons trouvé aucun lien entre le temps de floraison et la date de la fonte des neiges. Nos découvertes suggèrent que les effets écologiques sur la communauté biologique arctique conséquents aux changements de la phénologie causés par le changement climatique diffèreront de ceux dans les régions tempérées. [Traduit par la Rédaction]

Mots-clés : changement climatique, dryade à feuilles entières, saxifrage à feuilles opposées, ITEX, phénologie.

Introduction

Flowering times of many temperate spring flowering plants are advancing due to rising temperatures associated with recent climate change (Fitter et al. 1995; Abu-Asab et al. 2001; Primack et al. 2004; Beaubien and Hamann 2011; Panchen et al. 2012). Fruiting responses to climate change in temperate regions are less well studied and the changes less clear (Gordo and Sanz 2010; Gallinat et al. 2015). In temperate regions of Europe, some species are advancing their fruiting time due to rising temperatures of climate change (Menzel et al. 2006; Gordo and Sanz 2010; Van Vliet et al. 2014). However, in a North American study, the fruiting time of earlier-flowering species advanced with warmer temperatures, while the fruiting time of later-flowering species was delayed with warmer temperatures (Sherry et al. 2007). Temperatures in temperate regions have been rising since the 1960s, with increases being most pronounced during spring (Menne et al. 2010). Temperatures in the eastern Canadian Arctic, however, have been rising very rapidly since the 1990s but predominantly at the end of the summer and during winter (Przybylak 2003; McBean 2004; Furgal and Prowse 2007; AMAP 2011). In comparison to temperate regions, the different pattern and timing of climate change in the Arctic might result in different phenological responses of Arctic plants to climate change. By documenting Arctic phenological responses to climate change, we add to the picture of how plants respond to climate change.

Time of flowering is most often controlled by temperature or day length (photoperiod) or a combination of the two (Bernier and Périlleux 2005). Photoperiod control of flowering time is seen in some Arctic species but temperature is the main driver for Arctic plant flowering time (Porsild and Cody 1980; Thórhallsdóttir 1998; Keller and Körner 2003; Hülber et al. 2010). Vernalisation or a chilling period followed by a cumulative period of warmer temperatures (growing degree-days) controls time of flowering (Bernier and Périlleux 2005).

Unlike temperate regions, where there are many sources of long-term data on flowering and fruiting times of plants (Primack 2003; Primack and Miller-Rushing 2009; Culley 2013), the remoteness of the Arctic introduces challenges in obtaining long-term phenology data, and consequently, there are few data sets on the flowering and fruiting times of Arctic plants over an extended period of time (Høye et al. 2007*b*).

Parks Canada's Nunavut Field Unit established an International Tundra Experiment (ITEX) (Molau and Mølgaard 1996; Henry and Molau 1997) phenology monitoring program in 1994 at Quttinirpaaq National Park to monitor the flowering and fruiting times of purple saxifrage (*Saxifraga oppositifolia* L. (Saxifragaceae), aupilattunnguat (Inuktitut)) and mountain avens (*Dryas integrifolia* Vahl (Rosaceae), malikkaat (Inuktitut)) at the Tanquary Fiord warden station. *Saxifraga oppositifolia* and *D. integrifolia* are two common circumpolar Arctic plant species with a wide distribution across the Canadian Arctic Archipelago (Aiken et al. 2003; Elven 2003). These two species are often dominant in the Quttinirpaaq National Park landscape (Soper and Powell 1985; Edlund and Alt 1989). *Saxifraga oppositifolia* is one of the first Arctic plants to flower in spring, while *D. integrifolia* flowers in midsummer. The 20-year Tanquary Fiord ITEX phenology data set provides a unique opportunity to study how two species of Arctic plants that flower at different times during the growing season are responding to climate change.

With Arctic temperature changes occurring predominantly at the end of the growing season and winter, our hypothesis is that later-season flowering plants are flowering earlier

Fig. 1. International Tundra Experiment (ITEX) phenology monitoring area at Tanquary Fiord, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. (A) *Dryas integrifolia* tagged plants and (B) *Saxifraga oppositifolia* plant 19. The string is to aid in accurately counting the large number of flowers.

and Arctic plant fruits in general are maturing earlier, which we test herein with the *S. oppositifolia* and *D. integrifolia* Tanquary Fiord, Quttinripaaq National Park data set. We determine which monthly temperatures have the greatest influence on the time of flowering and fruiting of *S. oppositifolia and D. integrifolia*, whether snowmelt influences time of flowering of these two species, and whether temperatures in the previous year influence the quantity of flowers produced by these two species in the following year. We also address which monthly temperatures are rising at Tanquary Fiord.

Materials and methods

Site

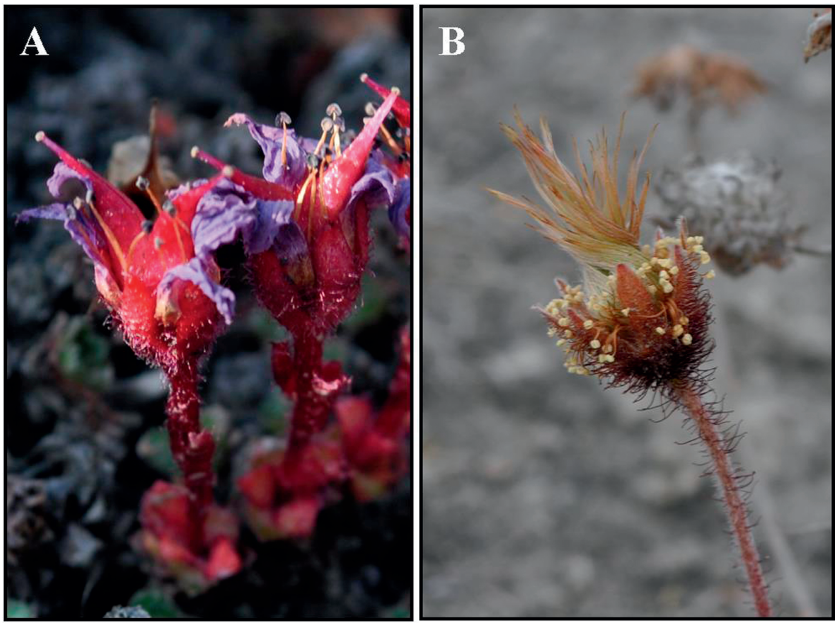
Quttinirpaaq National Park is situated on northern Ellesmere Island in the Canadian Arctic Archipelago. Tanquary Fiord is the name of the main warden station in the park and is located at the head of Tanquary Fiord at 81.4°N, 76.7°W. The region is a polar desert with mean annual precipitation of less than 50 mm (Edlund and Alt 1989; Przybylak 2003). The ITEX phenology plots are located on the edge of a gravel wash on the MacDonald River delta. The vegetation is discontinuous in the vicinity of the ITEX plots (Fig. 1A).

In 1994, Parks Canada's Nunavut Field Unit established two ITEX phenology monitoring 50 m × 50 m plots within a 15-min walk from the Tanquary Fiord warden station. The park staff randomly tagged 25 *S. oppositifolia* plants in the first plot and 25 *D. integrifolia* plants in the adjacent plot. The tagged plants ranged in diameter from 15 to 60 cm and were spaced at least 0.5 m apart (Fig. 1) (Raillard 1999).

Flowering and fruiting data

Every three days during spring and summer of 1994–2014, park staff recorded the number of flowers open on each tagged *S. oppositifolia* and *D. integrifolia* plant (Parks Canada 2002). A flower was considered open when the petals were open and the anthers visible. The protocol required that a flower be considered open until all of its petals dropped.

Fig. 2. (A) Mature fruit stage of *Saxifraga oppositifolia* and (B) twisted fruit stage of *Dryas integrifolia*.



Saxifraga oppositifolia flower counts started too late in 1994 to determine peak flower as the plots were set up during the midst of the *S. oppositifolia* flowering period. Not all plants flowered every year, and five *S. oppositifolia* plants appear to have died over the last 7 years of monitoring. The number of *S. oppositifolia* plants that flowered each year ranged from 18 to 25 except in 2001 when only 14 plants flowered. The mean number of *S. oppositifolia* plants that flowered each year was 22.25 with a standard deviation of 2.56. The number of *D. integrifolia* plants that flowered each year ranged from 19 to 25 except in 1998 when only 11 plants flowered. The mean number of *D. integrifolia* plants that flowered each year was 22.67 with a standard deviation of 3.00.

Every 3 days, park staff also counted the number of mature fruits on each *S. oppositifolia* plant and the number of twisted fruits on each *D. integrifolia* plant. A *S. oppositifolia* fruit was considered mature when its two carpels turned red and were swollen (Fig. 2A). A *D. integrifolia* fruit was considered to have twisted fruit when its styles had extended and twisted around each other (Fig. 2B). No mature fruit were recorded on the *S. oppositifolia* in 2009 and 2011. There were also no *D. integrifolia* twisted fruit counted in 1996.

For all 25 *S. oppositifolia* plants and separately for all 25 *D. integrifolia* plants, we summed the number of flowers and summed the number of fruits per visit per year. We determined peak flower and peak fruit day of year for each year for both species. We defined peak flower or fruit day of year as the number of days from 1st January to the day when the number of flowers or fruit first reached 90% of the maximum number of flowers or mature/twisted fruit counted that year. This ameliorated the problem in the protocol of requiring flowers to be counted until they dropped their petals. In the case of *S. oppositifolia* and, to a lesser extent *D. integrifolia*, petals persisted on plants well beyond anthesis (Fig. 2A), causing flowers to continue to be counted beyond the true open flower stage.

Temperature data

Parks Canada established a weather station at Tanquary Fiord in 1989. Temperature data from the weather station provided daily minimum, maximum, and mean temperatures from 1989 to 2002 and hourly temperatures from 2003 to 2014. We calculated the monthly mean minimum, monthly mean maximum, and monthly mean temperature by averaging the daily minimum, maximum, and mean temperatures for each month from 1989 to 2002. For 2003–2014, we first determined the daily minimum, maximum, and mean temperature from each day's hourly temperatures followed by averaging these daily minimum, maximum, and mean temperatures for each month. There were some months in which the Tanquary Fiord daily or hourly temperature data were incomplete. For months with incomplete temperature data, we reconstructed the Tanquary Fiord monthly temperatures from the Eureka, Ellesmere Island, Nunavut, Environment Canada Weather Station temperature data (Environment Canada 2014) using the method described by Leathers et al. (2008) and Panchen et al. (2012) (Table S1[1]). The Eureka Weather Station (79.59°N, 85.56°W) is the closest weather station to Tanquary Fiord and experiences a similar climate (Edlund and Alt 1989). We also calculated the annual mean minimum, annual mean maximum, and annual mean temperature from the monthly mean minimum, monthly mean maximum, and monthly mean temperatures.

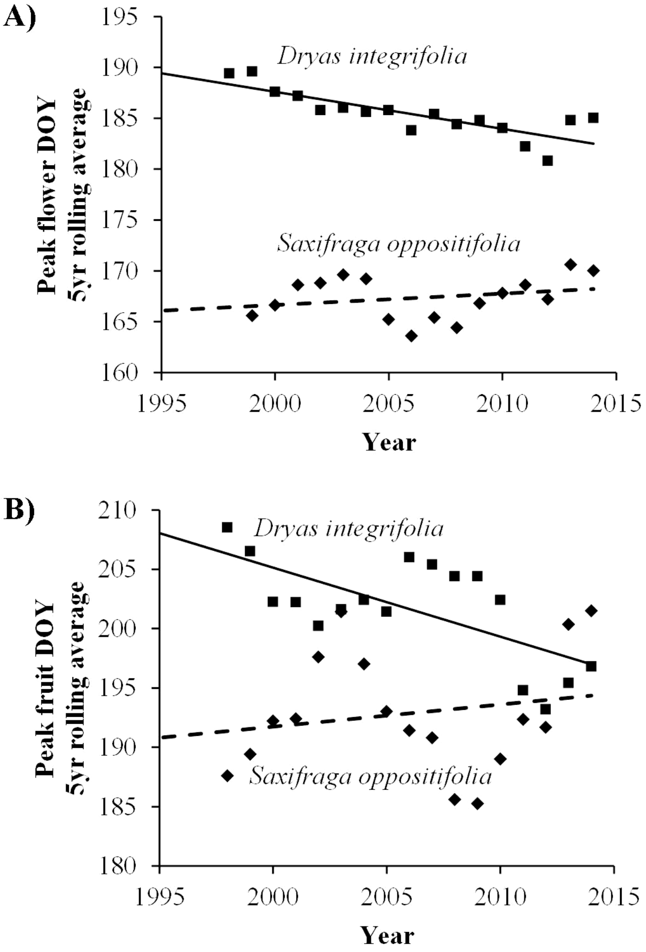
Statistical analysis

To account for interannual variation, we calculated the 5-year rolling average of peak flower and peak fruit day of year for each species each year from the species' yearly peak flower and peak fruit day of year. To determine the rate of change in flowering or fruiting time over the 20 years, we ran a regression analysis with the species' 5-year rolling average of peak flower or fruit day of year as the response variable and year as the independent variable. We also determined the year-to-year trend towards earlier flowering or fruiting by running a regression with the species' peak flower or fruit day of year as the response variable and year as the independent variable. We used a single standard least squares model per species to determine how much of the species' peak flower day of year was explained by year and April, May, June, and July mean temperatures and a similar model per species to explain the fruit day of year, i.e., peak flower or peak fruit day of year was the response variable and year and April, May, June, and July mean temperatures were the independent variables. To determine the rate of change in flowering or fruiting time with rising temperature for each species, a regression analysis was run with peak flower or fruit day of year as the response variable and June mean temperature as the independent variable for *D. integrifolia* and May mean temperature as the independent variable for *S. oppositifolia*. June and May temperatures were used because in the standard least squares models, June was the monthly temperature that had the greatest influence on the timing of flowering and fruiting for *D. integrifolia*, while May mean temperature had the greatest influence on the timing of flowering for *S. oppositifolia* (Table 1). To determine if time of flowering of each species is related to the snowmelt date, we ran a regression with peak flower day of year as the response variable and first snow-free date as the independent variable. We used a standard least squares model to determine how much of each species' peak flower count of one year was explained by June, July, August, and September mean minimum temperatures of the previous year, i.e., a single multiple regression for each species with peak flower count as the response variable and June, July, August, and September mean minimum temperatures as the independent variables. That is, does the previous year's summer or autumn temperatures affect the number of flowers that open in the following year? To determine the rate of rising temperatures over the past 25 years at Tanquary Fiord, we ran regressions of Tanquary Fiord annual and monthly mean minimum, mean maximum, and mean temperatures versus year. We also assessed the 1989–2014 average monthly temperature variation

---

[1] Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/as-2015-0016.

Fig. 3. (A) Peak flower and (B) peak fruit day of year (DOY) 5-year rolling average from 1994 to 2014 at Tanquary Fiord, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada, showing that *Dryas integrifolia* (squares and solid trend line) had a significant trend towards earlier flowering of 3.6 days/decade ($R^2 = 0.67$, $P < 0.0001$, $N = 17$) and earlier fruiting of 5.8 days/decade ($R^2 = 0.46$, $P = 0.003$, $N = 17$) but *Saxifraga oppositifolia* (diamonds and broken trend line) had no significant trend towards earlier flowering ($R^2 = 0.06$, $P = 0.3481$, $N = 16$) or earlier fruiting ($R^2 = 0.03$, $P = 0.4769$, $N = 17$).



through the year. We used the JMP11 software package (SAS Institute, Cary, North Carolina, USA) for all statistical analyses.

Results

Flowering and fruiting

The 5-year rolling average of peak flower and fruit day of year for *D. integrifolia* from 1994 to 2014 showed a significant trend towards earlier flowering and fruiting of 3.6 and 5.8 days/decade, respectively (flowering: $R^2 = 0.67$, $P < 0.0001$, $N = 17$ and fruiting: $R^2 = 0.46$, $P = 0.003$, $N = 17$) (Fig. 3). Without rolling averages, there was a year-to-year trend from 1994 to 2012 towards earlier flowering and fruiting for *D. integrifolia* of 5.2 and 8.9 days/decade, respectively (flowering: $R^2 = 0.27$, $P = 0.0223$, $N = 19$ and fruiting: $R^2 = 0.25$, $P = 0.0336$, $N = 18$). However, when the 2013 and 2014 data were added, the year-to-year trend towards earlier peak

Table 1. Standard least squares models showing how much of the *Dryas integrifolia* and *Saxifraga oppositifolia* peak flower and fruit day of year is explained by year and April, May, June, and July mean temperatures.

	Overall model			Year	April temperature	May temperature	June temperature	July temperature
	R^2	P	N	β (P)	β (P)	β (P)	β (P)	β (P)
Dryas integrifolia								
Peak flower day of year	0.77	0.0003	21	−0.05 (0.7278)	0.59 (0.0196)	−1.23 (0.0105)	−1.48 (0.0132)	−0.43 (0.3131)
Peak fruit day of year	0.60	0.0154	20	−0.34 (0.2565)	0.43 (0.3792)	0.83 (0.3606)	−3.65 (0.0050)	0.25 (0.7786)
Saxifraga oppositifolia								
Peak flower day of year	0.53	0.0429	20	0.26 (0.2215)	0.39 (0.2386)	−1.70 (0.0164)	−1.27 (0.1100)	0.62 (0.3080)
Peak fruit day of year	0.31	0.3653	19	0.26 (0.5481)	−1.16 (0.1467)	0.67 (0.6162)	−2.10 (0.2205)	1.08 (0.4708)

flowering and fruiting for *D. integrifolia* was not significant (flowering: $R^2 = 0.04$, $P = 0.3581$, $N = 21$ and fruiting: $R^2 = 0.08$, $P = 0.2313$, $N = 20$). The 5-year rolling average of peak flower and fruit day of year for *S. oppositifolia* showed no trend towards earlier flowering or fruiting (flowering: $R^2 = 0.06$, $P = 0.3481$, $N = 16$ and fruiting: $R^2 = 0.03$, $P = 0.4769$, $N = 17$) (Fig. 3). Likewise, without rolling averages, there remained no year-to-year trend towards earlier peak flowering or fruiting for *S. oppositifolia*.

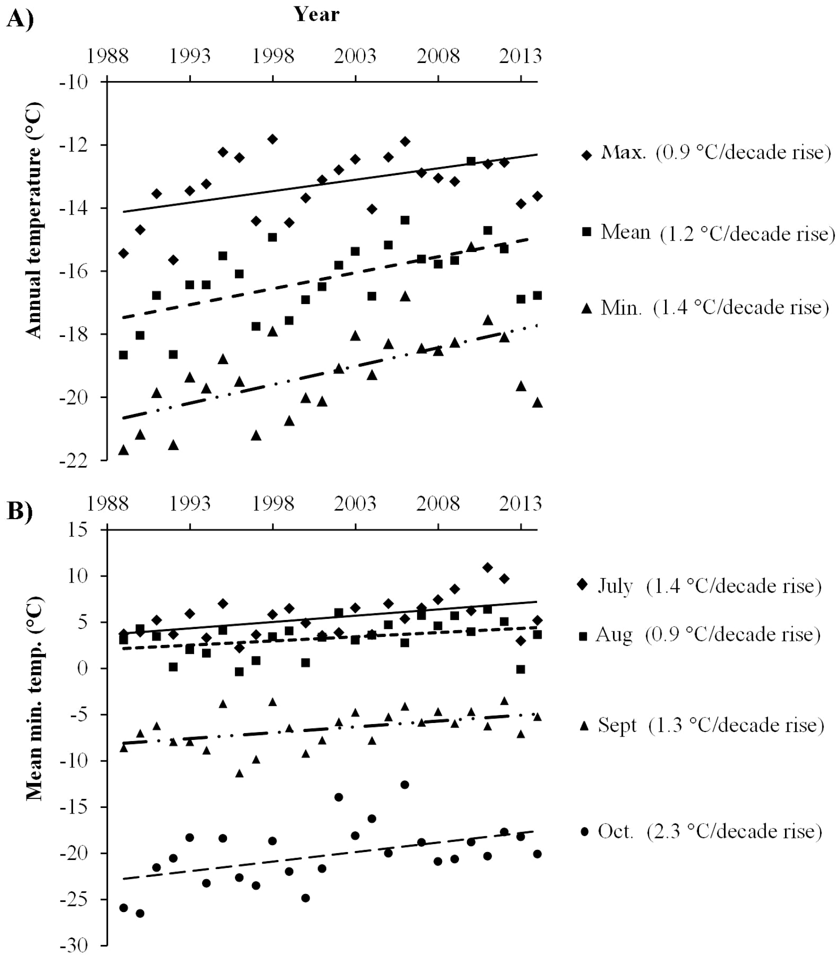
Much of the variation in *D. integrifolia* peak flower day of year was explained by year and April, May, June, and July mean temperatures (Table 1). *Dryas integrifolia* flowering time advances by 2.3 days/°C rise in June mean temperature ($R^2 = 0.54$, $P = 0.0001$, $N = 21$). Similarly, much of the variation in *D. integrifolia* peak fruit day of year was explained by year and April, May, June, and July mean temperatures, albeit with only June mean temperature as a significant term in the model (Table 1). *Dryas integrifolia* fruiting time advances by 3.4 days/°C rise in June temperature ($R^2 = 0.47$, $P = 0.0008$, $N = 20$). Some of the variation in *S. oppositifolia* peak flower day of year was explained by year and April, May, and June mean temperatures, albeit with only May mean temperature as the significant term in the model (Table 1). *Saxifraga oppositifolia* flowering time advances by 1.8 days/°C rise in May mean temperature ($R^2 = 0.30$, $P = 0.0127$, $N = 20$). However, no variation in *S. oppositifolia* peak fruit day of year was explained by year and monthly mean minimum temperatures (Table 1). There was no relationship between peak flower day of year and snowmelt date for either species (*S. oppositifolia*: $R^2 = 0.12$, $P = 0.1638$, $N = 18$ and *D. integrifolia*: $R^2 = 0.01$, $P = 0.6813$, $N = 18$).

Much of the variation in the peak number of *D. integrifolia* flowers is explained by the previous year's June, July, August, and September mean minimum temperatures ($R^2 = 0.47$, $P = 0.0316$, $N = 21$), with August mean minimum temperature as the only significant term in the model ($P = 0.0111$). There was a positive relationship between peak number of *S. oppositifolia* flowers and the previous year's October mean minimum temperatures ($R^2 = 0.27$, $P = 0.0188$, $N = 20$), although the model with the previous year's June, July, August, and September mean minimum temperatures as the independent variables was not significant ($R^2 = 0.13$, $P = 0.7072$, $N = 20$).

Temperature

The annual mean minimum, mean maximum, and mean temperatures at Tanquary Fiord have risen significantly over the past 25 years (Fig. 4A; Table 2). There is a significant trend towards warmer temperatures for January, March, July, August, September, and October (either at $\alpha = 0.05$ or $\alpha = 0.10$) (Fig. 4B; Table 2). The annual and monthly mean minimum temperatures are rising more than the annual and monthly mean maximum and mean temperatures (Fig. 4; Table 2).

Fig. 4. Change in temperatures from 1989 to 2014 at Tanquary Fiord, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. (A) Annual mean minimum, annual mean maximum, and annual mean temperatures and (B) July, August, September, and October mean minimum temperatures (Table 2).



The Tanquary Fiord average 1989–2014 monthly temperature varied little across the months of January, February, and March, hovering at approximately −35 °C (Fig. 5; Table S2). Temperatures rose dramatically in April and May to above zero by the start of June. Temperatures in June, July, and August varied between months by approximately 5 °C. Temperatures dropped dramatically in September and October and less steeply in November and December.

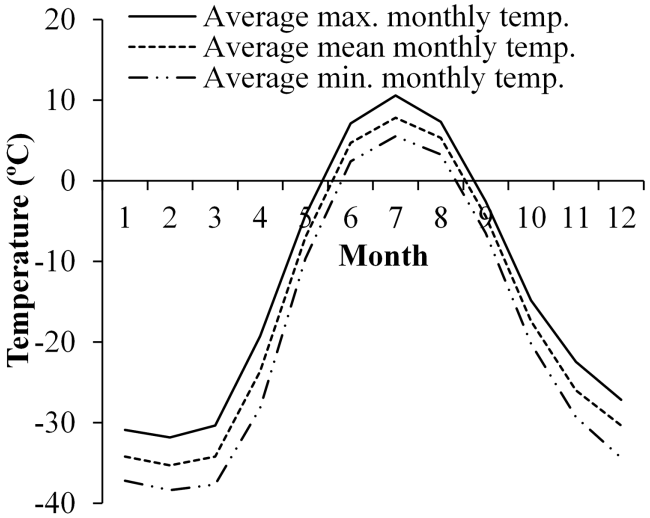
Discussion and conclusions

Flowering and fruiting times of the midsummer flowering *D. integrifolia* have advanced significantly over the 20 years from 1994 to 2014, but flowering and fruiting times of the early spring flowering *S. oppositifolia* have not changed significantly. This pattern is in striking contrast to temperate regions, in which it is predominantly spring-flowering plants that are flowering earlier, while summer-flowering plants and fruiting times are showing less of a trend towards earlier flowering and fruiting (Fitter et al. 1995; Abu-Asab et al. 2001; Primack et al. 2004; Menzel et al. 2006; Panchen et al. 2012). The earlier flowering of summer-, but not spring-, flowering species might be expected in the Arctic given that the

Table 2. Tanquary Fiord change in annual and monthly mean maximum, mean, and mean minimum temperatures from 1989 to 2014 (β = slope in °C/year, dark grey = significant at $\alpha = 0.05$, and pale grey = significant at $\alpha = 0.10$).

	Monthly mean maximum temperature (°C)			Monthly mean temperature (°C)			Monthly mean minimum temperature (°C)		
	R^2	P	β	R^2	P	β	R^2	P	β
January	0.19	0.025	0.248	0.25	0.010	0.266	0.29	0.005	0.274
February	0.00	0.810	0.027	0.02	0.540	0.062	0.04	0.320	0.093
March	0.08	0.156	0.158	0.14	0.056	0.198	0.18	0.032	0.214
April	0.06	0.213	−0.114	0.02	0.489	−0.063	0.00	0.747	−0.030
May	0.00	0.930	−0.006	0.00	0.793	0.016	0.01	0.677	0.027
June	0.00	0.901	0.007	0.01	0.697	0.021	0.02	0.483	0.035
July	0.13	0.076	0.093	0.15	0.054	0.117	0.24	0.011	0.137
August	0.12	0.079	0.090	0.14	0.057	0.097	0.13	0.067	0.091
September	0.08	0.163	0.061	0.15	0.047	0.094	0.22	0.015	0.127
October	0.18	0.037	0.153	0.24	0.014	0.197	0.26	0.009	0.233
November	0.03	0.440	0.068	0.05	0.271	0.095	0.09	0.154	0.012
December	0.04	0.324	0.129	0.06	0.257	0.139	0.08	0.166	0.159
Annual	0.27	0.008	0.086	0.41	<0.0001	0.120	0.47	0.0001	0.142

Fig. 5. Average (1989–2014) monthly mean minimum, monthly mean maximum, and monthly mean temperatures at Tanquary Fiord, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada (Table S2).



temperatures towards the end of the growing season are warming the most and flowering times are highly dependent on temperatures in the 1 or 2 months prior to flowering (Fitter et al. 1995; Thórhallsdóttir 1998; Panchen et al. 2012). Given that fall and winter temperatures are warming in the Arctic, the early spring flowering species *S. oppositifolia* may not be able to flower earlier because of vernalisation limitations (Cook et al. 2012*b*).

The advance in flowering time of *D. integrifolia* at Tanquary Fiord of 3.6 day/decade and 2.3 days/°C is comparable to spring flowering plants that are advancing the most in temperate northeastern North America (Bradley et al. 1999; Abu-Asab et al. 2001; Ledneva et al. 2004; Primack et al. 2004; Wolfe et al. 2005; Lavoie and Lachance 2006; Miller-Rushing and Primack 2008; Panchen et al. 2012), perhaps reflecting the rapid climate change that the Arctic is experiencing (McBean 2004; Høye et al. 2007*b*; AMAP 2011) and the greater sensitivity of colder climate plants (Cook et al. 2012*a*) but also indicating the substantial phenological plasticity of *D. integrifolia*. The above-noted differences in the pattern of phenological responses to climate change between the Arctic and temperate regions may result in different community-level ecological effects in Arctic versus temperate regions.

Our results also indicate that temperatures in the months just prior to flowering are most important in the timing of flowering. *Saxifraga oppositifolia* flowering time is primarily induced by temperatures 1 month prior to flowering, whereas *D. integrifolia* flowering is induced by the cumulative temperatures of the prior 3 months. *Dryas integrifolia* and *S. oppositifolia* also showed a difference in their flowering time temperature sensitivity (1.8 days/°C for *S. oppositifolia* versus 2.3 days/°C for *D. integrifolia*). Variation in phenological responses across taxa to a warming climate is a common finding across temperate, alpine, and Arctic regions (Fitter et al. 1995; Thórhallsdóttir 1998; Abu-Asab et al. 2001; Panchen et al. 2012; CaraDonna et al. 2014). The variation in flowering time temperature sensitivity plus the different monthly temperatures to which these two species showed flowering time temperature sensitivity may have implications for ecological community assembly, such as mismatches in timing between flowering time and pollinators (Hegland et al. 2009; McKinney et al. 2012; Høye et al. 2013). These differences in phenological responses to climate change of two species that dominate the landscape could also result in change of the dominant species in the ecological community assembly.

Our findings are consistent with a metadata analysis of the pan-Arctic ITEX data set using warmed and control plots and a long-term study in Swedish Lapland, which showed greater sensitivity to warming of later flowering species (Molau et al. 2005; Prevéy et al. 2014). Our findings are also consistent with a long-term study of flowering time in Iceland showing warming just prior to flowering as the main reason for earlier flowering (Thórhallsdóttir 1998). Studies with warmed and control plots and long-term phenology studies indicate a trend towards earlier flowering and fruiting for *D. integrifolia* and *Dryas octopetala* L., a congener and close relative of *D. integrifolia*, but no trend for *S. oppositifolia* (Wookey et al. 1993, 1995; Stenström et al. 1997; Welker et al. 1997; Molau 2001; Høye et al. 2007*a*; Cadieux et al. 2008; Ellebjerg et al. 2008). In addition, Keller and Körner (2003) found *S. oppositifolia* time of flowering not to be sensitive to either temperature or photoperiod, which also supports our findings of no trend towards earlier flowering time for *S. oppositifolia*. However, our findings differ from an ITEX study at Alexandra Fiord, Ellesmere Island, Nunavut, Canada, where summer-flowering plants trended towards later flowering (Bjorkman et al. 2015). This discrepancy could be a consequence of (1) monitoring start of flowering time, rather than peak flowering time, the former of which typically has more variation (Miller-Rushing et al. 2008), (2) experimental warming studies underprediction of responses to climate change (Wolkovich et al. 2012), or (3) a possible increase in snow accumulation over the study period at Alexandra Fiord (Bjorkman et al. 2015).

Twenty years, however, appears to be too short of a time period to see a consistent year-to-year trend in earlier flowering or fruiting times. In comparison to the previous decade, 2013 was exceptionally cold and snowy in the Canadian Arctic Archipelago (Fig. 4B). The addition of the 2013 flowering and fruiting data to the analysis therefore, not too surprisingly, eliminated the earlier flowering and fruiting trend that had been seen in *D. integrifolia* up until 2012. However, the rolling average, which accounts for interannual variation, showed *D. integrifolia*' flowering and fruiting times advancing with the inclusion of the 2013 data. This should come as no surprise insofar as multiyear moving averages smooth through single-year anomalies. It will be interesting to see what the next few years of temperature and phenology data tell us about the trend of *D. integrifolia* towards earlier flowering and fruiting.

Because Arctic temperature rises are predominantly occurring at the end of the growing season (and winter), we had expected to see earlier fruiting times for *S. oppositifolia* as well as *D. integrifolia*. An earlier fruiting trend for *S. oppositifolia* might have been masked by the fact that ripening fruits continued to be counted as open flowers even when the petals were wilted because the Tanquary Fiord ITEX protocol required counting something as an open flower until the petals dropped. *Saxifraga oppositifolia* petals persist into the fruiting stage and hence, some mature fruits may have been counted as open flowers when they should have been counted as mature fruits. The protocol has now been changed and the use of the method whereby the peak flowering date is assumed to be the date of 90% of the maximum flower counts will enable the data to be analysed consistently across the pre- and post-protocol change.

In contrast to some alpine and Arctic studies (e.g., Høye et al. 2007*a*; Anderson et al. 2012), but in agreement with others (e.g., Kudo and Hirao 2006; Kimball et al. 2014), we found no relationship between flowering time and snowmelt date for *S. oppositifolia* and *D. integrifolia*. This could perhaps be because snow accumulation at Tanqaury Fiord is low, with less than 50 mm precipitation per year (Edlund and Alt 1989; Thompson 1994; Przybylak 2003). Similarly, a long-term study in the central highlands of Iceland, another polar desert region, also found no relationship between time of flowering and snowmelt date except in two years with high snow accumulation (Thórhallsdóttir 1998). The lack of a relationship between flowering time and snowmelt date could also be an artifact of the arrival time of park staff who, in some years, arrived too late to record an accurate first snow-free day.

At Tanquary Fiord, the previous year's late-summer temperatures were correlated with the number of *D. integrifolia* flowers opening the following year. This is to be expected because Arctic plants preform their flower buds in the year or years prior to flowering, presumably to maximise reproductive success in the very short Arctic growing season (Sørensen 1941). Given the dependence on the prior year's temperatures to form flower buds for the next year, extreme events and more varied climates could be problematic for reproductive success of Arctic plants (Inouye and McGuire 1991; Inouye 2008). The correlation of the number of *S. oppositifolia* flowers with the previous year's October mean minimum temperatures may indicate a greater susceptibility of *S. oppositifolia* flower buds to cold damage because the flower buds are aboveground, while *D. integrifolia* flower buds are belowground. There is likely little snow in October at Tanquary Fiord to insulate and protect the aboveground buds of *S. oppositifolia* when the temperatures drop dramatically (Fig. 5).

The sampling protocol used in this monitoring program was to select 25 plants at the start of the monitoring program and monitor these same plants each year. The disadvantage, as was seen at Tanquary Fiord, is that Arctic plants do not flower every year and some of the plants may die, reducing the yearly sample size. Nevertheless, with the exception of one year for each species, the sample size remained reasonably close to the original sample size across the 20-year period. An alternative approach is to select 25 plants each year that have indications that they will flower to ensure a more consistent sample size each year. However, the alternative approach could bias the results towards earlier-flowering plants, is more labour intensive than the approach used at Tanquary Fiord, introduces variance in the time series due to different phenotypes of the individual plants, and could introduce inconsistencies in the plant selection method from year to year. The advantage of the approach used at Tanquary Fiord is that it is less labour intensive than the alternative approach and the selected sample is consistent year after year and eliminates variation in the time series due to individual plant phenotypes.

Unlike temperate regions, but comparable to the Arctic in general, the most significant warming at Tanquary Fiord is towards the end of the growing season and during the winter (Przybylak 2003; McBean 2004; Furgal and Prowse 2007; AMAP 2011). Tanquary Fiord's monthly mean minimum temperatures are rising more than the monthly mean maximum temperatures and monthly mean temperatures. Monthly mean minimum temperatures are also rising more than monthly mean maximum temperatures and monthly mean temperatures in temperate regions (Menne et al. 2010).

Our study indicates a different pattern in the response of Arctic plants to a warming climate compared to temperate regions, with the midsummer flowering species *D. integrifolia* trending towards earlier flowering and fruiting, but the early spring flowering species *S. oppositifolia* showing no trend towards earlier flowering and fruiting. Hence, changes in ecological and community-level interactions could play out differently in the Arctic than in temperate regions (Hegland et al. 2009; McKinney et al. 2012; Høye et al. 2013).

Acknowledgements

The authors wish to thank Parks Canada's Nunavut Field Unit for providing the Tanquary Fiord ITEX phenology and temperature data and their in-kind support of the research and Quttinirpaaq National Park staff for gathering the data. The authors are also grateful to the Hamlets and Hunter and Trapper Organisations of Grise Fiord and Resolute for their support of the research. This research was funded by a Natural Sciences and Engineering Research Council of Canada Canadian Graduate Scholarship (NSERC CGS) to Z.P. and a Natural Sciences and Engineering Research Council of Canada Discovery Grant to R.G.

References

Abu-Asab, M., Peterson, P., Shetler, S., and Orli, S. 2001. Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. Biodivers. Conserv. **10**: 597–612. doi: 10.1023/A:1016667125469.

Aiken, S.G., Dallwitz, M.J., Consaul, L.L., Mcjannet, C.L., Boles, R.L., Argus, G.W., Gillett, J.M., Scott, P.J., Elven, R., Leblanc, M.C., Gillespie, L.J., Brysting, A.K., Solstad, H., and Harris, J.G. 2003. Flora of the Canadian Arctic Archipelago. Available from http://nature.ca/aaflora/data/aaintro/caaintr2.htm [accessed February 2015].

AMAP. 2011. Snow, water, ice and permafrost in the arctic (SWIPA): climate change in the arctic—a hot topic. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.

Anderson, J.T., Inouye, D.W., Mckinney, A.M., Colautti, R.I., and Mitchell-Olds, T. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proc. Biol. Sci. **279**: 3843–3852. PMID: 22787021. doi: 10.1098/rspb.2012.1051.

Beaubien, E., and Hamann, A. 2011. Spring flowering response to climate change between 1936 and 2006 in Alberta, Canada. BioScience, **61**: 514–524. doi: 10.1525/bio.2011.61.7.6.

Bernier, G., and Périlleux, C. 2005. A physiological overview of the genetics of flowering time control. Plant Biotechnol. J. **3**: 3–16. PMID: 17168895. doi: 10.1111/j.1467-7652.2004.00114.x.

Bjorkman, A., Elmendorf, S.C., Beamish, A.L., Henry, G.H.R., and Vellend, M. 2015. Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. Glob. Change Biol. PMID: 26216538. doi: 10.1111/gcb.13051.

Bradley, N.L., Leopold, A.C., Ross, J., and Wellington, H. 1999. Phenological changes reflect climate change in Wisconsin. Proc. Natl. Acad. Sci. U.S.A. **96**: 9701–9704.

Cadieux, M.-C., Gauthier, G., Gagnon, C.A., Lévesque, E., Bêty, J., and Berteaux, D. 2008. Monitoring the environmental and ecological impacts of climate change on Bylot Island, Sirmilik National Park 2004–2008 final report. Centre d'Études Nordiques, Université Laval, Québec, Qué.

Caradonna, P.J., Iler, A.M., and Inouye, D.W. 2014. Shifts in flowering phenology reshape a subalpine plant community. Proc. Natl. Acad. Sci. U.S.A. **111**: 4916–4921. doi: 10.1073/pnas.1323073111.

Cook, B.I., Wolkovich, E.M., Davies, T.J., Ault, T.R., Betancourt, J.L., Allen, J.M., Bolmgren, K., Cleland, E.E., Crimmins, T.M., Kraft, N.J.B., Lancaster, L.T., Mazer, S.J., Mccabe, G.J., Mcgill, B.J., Parmesan, C., Pau, S., Regetz, J., Salamin, N., Schwartz, M.D., and Travers, S.E. 2012*a*. Sensitivity of spring phenology to warming across temporal and spatial climate gradients in two independent databases. Ecosystems, **15**: 1283–1294. doi: 10.1007/s10021-012-9584-5.

Cook, B.I., Wolkovich, E.M., and Parmesan, C. 2012*b*. Divergent responses to spring and winter warming drive community level flowering trends. Proc. Natl. Acad. Sci. U.S.A. **109**: 9000–9005. doi: 10.1073/pnas.1118364109.

Culley, T.M. 2013. Why vouchers matter in botanical research. Appl. Plant Sci. **1**: 1300076. PMID: 25202501. doi: 10.3732/apps.1300076.

Edlund, S.A., and Alt, B.T. 1989. Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada. Arctic. **42**: 3–23. doi: 10.14430/arctic1635.

Ellebjerg, S.M., Tamstorf, M.P., Illeris, L., Michelsen, A., and Hansen, B.U. 2008. Inter-annual variability and controls of plant phenology and productivity at Zackenberg. *In* High-Arctic ecosystem dynamics in a changing climate. *Edited by* H. Meltofte, T. Christensen, B. Elberling, M. Forchhammer, and M. Rasch. Academic Press, London, U.K. pp. 249–272.

Elven, R. 2003. Annotated checklist of the pan-arctic flora (PAF) vascular plants. Available from http://nhm2.uio.no/paf/ [accessed February 2015].

Environment Canada. 2014. National climate data and information archive. Available from http://www.climate.weatheroffice.gc.ca/climateData/canada_e.html [accessed December 2014].

Fitter, A.H., Fitter, R.S.R., Harris, I.T.B., and Williamson, M.H. 1995. Relationships between first flowering date and temperature in the flora of a locality in central England. Funct. Ecol. **9**: 55–60. doi: 10.2307/2390090.

Furgal, C., and Prowse, T.D. 2007. Northern Canada. *In* From impacts to adaptation: Canada in a changing climate. *Edited by* D.S. Lemmen, F.J. Warren, and J. Lacroix. Natural Resources Canada, Ottawa, Ont. pp. 57–118.

Gallinat, A.S., Primack, R.B., and Wagner, D.L. 2015. Autumn, the neglected season in climate change research. Trends Ecol. Evol. **30**: 169–176. doi: 10.1016/j.tree.2015.01.004.

Gordo, O., and Sanz, J.J. 2010. Impact of climate change on plant phenology in Mediterranean ecosystems. Glob. Change Biol. **16**: 1082–1106. doi: 10.1111/j.1365-2486.2009.02084.x.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L., and Totland, Ø. 2009. How does climate warming affect plant–pollinator interactions? Ecol. Lett. **12**: 184–195. PMID: 19049509. doi: 10.1111/j.1461-0248.2008.01269.x.

Henry, G.H.R., and Molau, U. 1997. Tundra plants and climate change: the International Tundra Experiment (ITEX). Glob. Change Biol. **3**: 1–9.

Høye, T.T., Mølgaard Ellebjerg, S., and Philipp, M. 2007*a*. The impact of climate on flowering in the high Arctic — the case of *Dryas* in a hybrid zone. Arct. Antarct. Alpine Res. **39**: 412–421. doi: 10.1657/1523-0430(06-018)[HOYE]2.0.CO;2.

Høye, T.T., Post, E., Meltofte, H., Schmidt, N.M., and Forchhammer, M.C. 2007*b*. Rapid advancement of spring in the High Arctic. Curr. Biol. **17**: 449–451. doi: 10.1016/j.cub.2007.04.047.

Høye, T.T., Post, E., Schmidt, N.M., Trøjelsgaard, K., and Forchhammer, M.C. 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. Nat. Clim. Change. **3**: 759–763. doi: 10.1038/nclimate1909.

Hülber, K., Winkler, M., and Grabherr, G. 2010. Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species. Funct. Ecol. **24**: 245–252. doi: 10.1111/j.1365-2435.2009.01645.x.

Inouye, D.W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology, **89**: 353–362. PMID: 18409425. doi: 10.1890/06-2128.1.

Inouye, D.W., and Mcguire, A.D. 1991. Effects of snowpack on timing and abundance of flowering in *Delphinium nelsonii* (Ranunculaceae): implications for climate change. Am. J. Bot. **78**: 997–1001.

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

Kimball, K.D., Davis, M.L., Weihrauch, D.M., Murray, G.L.D., and Rancourt, K. 2014. Limited alpine climatic warming and modeled phenology advancement for three alpine species in the Northeast United States. Am. J. Bot. **101**: 1437–1446. PMID: 25253704. doi: 10.3732/ajb.1400214.

Kudo, G., and Hirao, A.S. 2006. Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts. Popul. Ecol. **48**: 49–58. doi: 10.1007/s10144-005-0242-z.

Lavoie, C., and Lachance, D. 2006. A new herbarium-based method for reconstructing the phenology of plant species across large areas. Am. J. Bot. **93**: 512–516. doi: 10.3732/ajb.93.4.512.

Leathers, D.J., Malin, M.L., Kluver, D.B., Henderson, G.R., and Bogart, T.A. 2008. Hydroclimatic variability across the Susquehanna River Basin, USA, since the 17th century. Int. J. Climatol. **28**: 1615–1626. doi: 10.1002/joc.1668.

Ledneva, A., Miller-Rushing, A.J., Primack, R.B., and Imbres, C. 2004. Climate change as reflected in a naturalist's diary, Middleborough, Massachusetts. Wil. Bull. **116**: 224–231.

McBean, G. 2004. Arctic climate: past and present. *In* Impacts of a warming Arctic: Arctic climate impact assessment. *Edited by* S. Hassol. Cambridge University Press, Cambridge, U.K. pp. 21–60.

McKinney, A.M., Caradonna, P.J., Inouye, D.W., Barr, B., Bertelsen, C.D., and Waser, N.M. 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. Ecology. **93**: 1987–1993. PMID: 23094369. doi: 10.1890/12-0255.1.

Menne, M.J., Williams, C.N., and Vose, R.S. 2010. Long term daily and monthly climate records from stations across the contiguous United States. Available from http://cdiac.ornl.gov/epubs/ndp/ushcn/access.html [accessed September 2013].

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remisová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F., Zach, S., and Zust, A. 2006. European phenological response to climate change matches the warming pattern. Glob. Change Biol. **12**: 1969–1976. doi: 10.1111/j.1365-2486.2006.01193.x.

Miller-Rushing, A.J., and Primack, R.B. 2008. Global warming and flowering times in Thoreau's Concord: a community perspective. Ecology. **89**: 332–341. PMID: 18409423.

Miller-Rushing, A.J., Inouye, D.W., and Primack, R.B. 2008. How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. J. Ecol. **96**: 1289–1296. doi: 10.1111/j.1365-2745.2008.01436.x.

Molau, U. 2001. Tundra plant responses to experimental and natural temperature changes. Mem. Nat. Inst. Polar Res. **54**: 445–466.

Molau, U., and Mølgaard, P. 1996. ITEX manual. Danish Polar Centre, Denmark.

Molau, U., Nordenhäll, U., and Eriksen, B. 2005. Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. Am. J. Bot. **92**: 422–431. PMID: 21652418. doi: 10.3732/ajb.92.3.422.

Panchen, Z.A., Primack, R.B., Anisko, T., and Lyons, R. 2012. Herbarium specimens, photographs and field observations show Philadelphia area plants are responding to climate change. Am. J. Bot. **99**: 751–756. PMID: 22447982. doi: 10.3732/ajb.1100198.

Parks Canada. 2002. QNP ITEX field protocol. Nunavut Field Unit, Parks Canada.

Porsild, A.E., and Cody, W.J. 1980. Vascular plants of continental Northwest Territories, Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ont.

Prevéy, J., Rixen, C., Hollister, R., Henry, G., Welker, J., Molau, U., Levesque, E., Oberbauer, S., Troxler, T., Elmendorf, S., Wipf, S., Hoye, T., Bjorkman, A., and Myers-Smith, I. 2014. Flowering time and historical climate help explain phenological responses of Arctic and alpine plants to climate change. International Arctic Change 2014 Conference. pp. 155–156.

Primack, R.B. 2003. The special role of historical plant records in monitoring the impact of climate change. Arnoldia, **62**: 12–15.

Primack, D., Imbres, C., Primack, R.B., Miller-Rushing, A.J., and Del Tredici, P. 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. Am. J. Bot. **91**: 1260–1264. PMID: 21653483. doi: 10.3732/ajb.91.8.1260.

Primack, R.B., and Miller-Rushing, A.J. 2009. The role of botanical gardens in climate change research. New Phytol. **182**: 303–313. PMID: 19338634. doi: 10.1111/j.1469-8137.2009.02800.x.

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

Raillard, M. 1999. Plant phenology monitoring protocol. Western Arctic Field Unit, Parks Canada.

Sherry, R.A., Zhou, X., Gu, S., Arnone, J.A., Schimel, D.S., Verburg, P.S., Wallace, L.L., and Luo, Y. 2007. Divergence of reproductive phenology under climate warming. Proc. Natl. Acad. Sci. U.S.A. **104**: 198–202. doi: 10.1073/pnas.0605642104.

Soper, J.H., and Powell, J.M. 1985. Botanical studies in the Lake Hazen region, Northern Ellesmere Island, Northwest Territories, Canada. Publ. Nat. Sci. **5**: 1–67.

Sørensen, T.J. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. C.A. Reitzel, Meddelelser om Grønland.

Stenström, M., Gugerli, F., and Henry, G.H.R. 1997. Response of *Saxifraga oppositifolia* L. to simulated climate change at three contrasting latitudes. Glob. Change Biol. **3**: 44–54. doi: 10.1111/j.1365-2486.1997.gcb144.x.

Thompson, W. 1994. Climate. *In* Resource description and analysis: Ellesmere Island, National Park Reserve. *Edited by* W. Thompson. National Resource Conservation Section, Prairie and Northern Region, Parks Canada, Department of Canadian Heritage, Winnipeg, Man. pp. 1–78.

Thórhallsdóttir, T. 1998. Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. Oecologia, **114**: 43–49. doi: 10.1007/s004420050418.

Van Vliet, A.J.H., Bron, W.A., Mulder, S., van der Slikke, W., and Ode, B. 2014. Observed climate-induced changes in plant phenology in the Netherlands. Reg. Environ. Change **14**: 997–1008. doi: 10.1007/s10113-013-0493-8.

Welker, J.M., Molau, U., Parsons, A.N., Robinson, C.H., and Wookey, P.A. 1997. Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. Glob. Change Biol. **3**: 61–73. doi: 10.1111/j.1365-2486.1997.gcb143.x.

Wolfe, D.W., Schwartz, M.D., Lakso, A.N., Otsuki, Y., Pool, R.M., and Shaulis, N.J. 2005. Climate change and shifts in spring phenology of three horticultural woody perennials in northeastern USA. Int. J. Biometeorol. **49**: 303–309. doi: 10.1007/s00484-004-0248-9.

Wolkovich, E.M., Cook, B.I., Allen, J.M., Crimmins, T.M., Betancourt, J.L., Travers, S.E., Pau, S., Regetz, J., Davies, T.J., Kraft, N.J.B., Ault, T.R., Bolmgren, K., Mazer, S.J., McCabe, G.J., McGill, B.J., Parmesan, C., Salamin, N., Schwartz, M. D., and Cleland, E.E. 2012. Warming experiments underpredict plant phenological responses to climate change. Nature, **485**: 494–497. doi: 10.1038/nature11014.

Wookey, P.A., Parsons, A.N., Welker, J.M., Potter, J.A., Callaghan, T.V., Lee, J.A., and Press, M.C. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-Arctic and high Arctic plants. Oikos, **67**: 490–502. doi: 10.2307/3545361.

Wookey, P.A., Robinson, C.H., Parsons, A.N., Welker, J.M., Press, M.C., Callaghan, T.V., and Lee, J.A. 1995. Environmental constraints on the growth, photosynthesis and reproductive development of *Dryas octopetala* at a high Arctic polar semi-desert, Svalbard. Oecologia, **102**: 478–489. doi: 10.1007/BF00341360.