

The impact of climate change on the flowering and fruiting
phenology of Arctic plants in Nunavut, Canada

by

Zoe Panchen

A thesis submitted to the Faculty of Graduate and Postdoctoral
Affairs in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Biology

Carleton University
Ottawa, Ontario

2016

Zoe Panchen

Abstract

Phenology is the timing of nature's seasonal events. Ambient temperature plays a key role in phenology and hence, as the climate warms, phenology will likely change. This thesis studied the impact of Arctic climate change on Arctic plant flowering and fruiting phenology in Nunavut, Canada. To establish a baseline for current plant phenology, the first question asked was 'How does flowering phenology vary across Nunavut?'

Contrary to what might be expected, plants at a more northerly location flower earlier or at the same time and for a shorter duration than conspecifics at a more southerly location.

Observations of vast differences in flower abundance in three consecutive and climatically-contrasting years highlighted the challenges of reproductive success with weather extremes associated with contemporary climate change given that Arctic plants require three plus years to complete the sexual reproductive cycle. Finally, three methods, employing long-term phenology monitoring, historical phenological records and an elevation gradient, combined with temperature records, were used to ask the questions: 'How have temperatures in Nunavut changed?', 'How have Nunavut Arctic flowering and fruiting times responded to climate change?' and 'What is the predicted temperature-sensitivity of Arctic plants to rising temperatures of climate change?'. Annual temperatures in Nunavut are rising faster than the global average. However, in contrast to temperate regions where spring temperatures are rising the most, monthly temperatures in late summer, autumn and winter are rising significantly in Nunavut. Later-flowering species have advanced flowering times more than early-flowering species and seed dispersal times have advanced more than flowering times. Flowering time temperature-sensitivity is species specific and Nunavut region specific with mid-summer-flowering

species more sensitive than early- and late-flowering species and Nunavut Arctic archipelago plants more sensitive than Nunavut mainland conspecifics. That Arctic plants' reproductive phenological events are temperature-sensitive is a good news story suggesting that they will respond to climate change and possibly experience greater reproductive success. Interspecific and inter-regional variation in phenological temperature-sensitivity suggests Arctic plant ecological community structure will alter with climate change but differentially across Nunavut.

Preface

This thesis contains five data chapters. Chapters 2, 3 and 4 are published and Chapters 5 and 6 are in review at refereed journals. I am the sole author of Chapters 3 and 6, while Chapters 2, 4 and 5 were co-authored with my thesis advisor, Dr. Root Gorelick. For all five data chapters I conceived the ideas, designed the studies, collected the data, ran the analysis and wrote the manuscripts. Dr. Root Gorelick provided guidance in his advisory role and editorial suggestions for the manuscripts. All published chapters are included in their entirety in this thesis with minor modification to correct grammar and typos, and provide minor clarifications requested by the thesis examining committee.

Chapter 2 is in press as PANCHEN, Z.A. and R. GORELICK. 2016. Canadian Arctic Archipelago conspecifics flower earlier in the High Arctic than the mid-Arctic.

International Journal of Plant Sciences. DOI 10.1086/687984. Reprinted in this thesis with permission from The University of Chicago Press

Chapter 3 is published as PANCHEN, Z.A. 2016. Arctic plants produce vastly different numbers of flowers in three contrasting years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. *Canadian Field-Naturalist* 130: 56–63. Reprinted in this thesis with permission from Ottawa Field-Naturalists' Club.

Chapter 4 is published as PANCHEN, Z.A. and 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 Science* 1: 45–58. DOI 10.1139 /AS-2015-0016. Reprinted in this thesis with permission from Canadian Science Publishing.

Chapter 5 is in review at *Ecology and Evolution* as PANCHEN, Z.A. and R.

GORELICK. Prediction of Arctic plant phenological sensitivity to climate change from historical records.

Chapter 6 is in review at *Polar Biology* as PANCHEN, Z.A. Space for time: Arctic plant phenological responses to climate change, substituting an elevation gradient as a proxy for the rising temperatures of climate change.

Acknowledgements

I would like to thank Dr. Root Gorelick for guiding me through all the ups and downs that is a Ph.D.; his pearls of wisdom were timely, insightful and helpful. I would also like to thank my thesis committee members, Dr. Christopher Burn and Dr. Lynn Gillespie, for their sage advice; their extensive Arctic expertise was valuable in building my knowledge on Arctic climate and Arctic plants and preparing me for my field seasons. I thank Dr. David Inouye and Dr. Brett Stevens for their roles as external examiners of my thesis and for their thoughtful questions during the defense.

I feel fortunate and privileged to have had the opportunity to visit and work in Nunavut and I thank the Hamlets and Hunter and Trapper Organisations of Grise Fiord, Iqaluit and Resolute for supporting my research on Inuit land.

Over my three years of Arctic field work, my field assistants, Sophia Jain-Schlaepfer, Orla Osborne, Emma Micalizzi, Joan Makaroff, Teresa Tufts and Carly Casey did a stellar job of assisting me with data collection, enduring sometimes less than ideal weather and bugs, and counting more flowers than they would care to remember.

At Carleton University I received support and advice from many faculty and peers and I'd like to particularly thank Andrew Simons, Derek Mueller, Joe Bennet, Richard Webster, Tom Hossie, Dani Fraser, Lindsey Derraugh and Felipe Dargent. Outside of the University I received advice and help from Bea Alt, Jennifer Doubt at the Canadian Museum of Nature, Jason Carpenter at Nunavut's Arctic College, Paul Smith at NWRC, Kyra St. Pierre at the University of Calgary and staff at the National Herbarium of Canada (CAN), Agriculture Canada Vascular Plant Herbarium (DAO), Herbarium Louis-Marie (QFA) and University of Toronto at Mississauga Herbarium (TRTE). Some of

those listed above and the Primack lab, Jeff Saarela, Paul Sokoloff, Johann Wagner and several anonymous reviewers took the time to review some of my manuscripts and I thank them for improving the manuscripts and helping me become a better writer.

I received funding from many sources without which, I would not have been able to conduct field work in one of the remotest regions of the Arctic. I would like to thank the following for their financial support: Scholarships: Arctic Institute of North America (Jennifer Robinson Memorial Scholarship); Canadian Federation of University Women (Beverley Jackson Fellowship); Carleton University; Natural Sciences and Engineering Research Council (NSERC); and Ontario Graduate Scholarship (OGS) Program. Grants and travel bursaries: Carleton University; Northern Scientific Training Program (NSTP); and Polar Continental Shelf Program (PCSP). In kind support: 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.

Finally, but not least, I would like to thank Chris Macknie for his support and encouragement to the 'perpetual student'.

Table of Contents

Abstract.....	ii
Preface.....	iv
Acknowledgements	vi
List of Tables	xi
List of Figures.....	xv
List of Appendices.....	xxi
1 Chapter: Introduction	1
1.1 Arctic climate and climate change in the Canadian Arctic.....	3
1.2 Plant reproductive phenology in a changing climate.....	6
1.3 Arctic plant reproductive phenology and temperature	9
1.4 Thesis Overview	12
2 Chapter: Canadian Arctic Archipelago conspecifics flower earlier in the High Arctic than the mid-Arctic	16
2.1 Abstract	16
2.2 Introduction	17
2.3 Materials and methods.....	19
2.3.1 Locations.....	19
2.3.2 Flowering phenology monitoring.....	21
2.3.3 Temperature	23
2.3.4 Statistical analysis	23
2.4 Results	25
2.5 Discussion.....	31

3 Chapter: Arctic plants produce vastly different numbers of flowers in three contrasting years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada	37
3.1 Abstract	37
3.2 Introduction	37
3.3 Materials and methods.....	40
3.4 Results	43
3.5 Discussion.....	47
4 Chapter: Flowering and fruiting responses to climate change of two Arctic plant species, purple saxifrage (<i>Saxifraga oppositifolia</i>) and mountain avens (<i>Dryas integrifolia</i>).....	51
4.1 Abstract	51
4.2 Introduction	52
4.3 Materials and methods.....	54
4.3.1 Site	54
4.3.2 Flowering and fruiting data.....	55
4.3.3 Temperature data.....	57
4.3.4 Statistical analysis	58
4.4 Results	60
4.4.1 Flowering and fruiting.....	60
4.4.2 Temperature	62
4.5 Discussion.....	65
5 Chapter: Prediction of Arctic plant phenological sensitivity to climate change from historical records	72
5.1 Abstract	72
5.2 Introduction	73
5.3 Materials and methods.....	76

5.3.1	Flowering time and seed dispersal time data	76
5.3.2	Temperature data.....	79
5.3.3	Analysis.....	80
5.4	Results	82
5.5	Discussion.....	93
6	Chapter: Space for time: Arctic plant phenological responses to climate change, substituting an elevation gradient as a proxy for the rising temperatures of climate change.....	98
6.1	Abstract	98
6.2	Introduction	99
6.3	Materials and methods.....	100
6.3.1	Field sites	100
6.3.2	Flowering and seed dispersal data.....	101
6.3.3	Temperature data.....	102
6.3.4	Analysis.....	102
6.4	Results	103
6.5	Discussion.....	108
7	Chapter: Conclusion.....	112
	References.....	116
	Appendices.....	141
A.1	Chapter 2 Supplementary Tables and Figures.....	141
A.2	Chapter 4 Supplementary Tables	146
A.3	Chapter 5 Supplementary Tables	149

List of Tables

Table 2.1. Iqaluit and Eureka Environment Canada Weather Stations' 30-year mean, 2013 and 2014 May to August mean temperatures (°C) and 30-year mean annual snowfall, number of days in June with a snow depth greater than or equal to 1cm and annual degree days above zero (Environment Canada 2016). The Eureka weather station is the closest weather station to Lake Hazen, Ellesmere Island, Nunavut and experiences a similar climate (Edlund and Alt 1989; Thompson 1994). Reprinted with permission from The University of Chicago Press.	21
Table 2.2. 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 negative value indicates that the Lake Hazen species flowered earlier or for a shorter duration ($***P < 0.0001$, $**P < 0.001$, $*P < 0.05$). Reprinted with permission from The University of Chicago Press.	28
Table 2.3. Linear mixed effects model results with species as a random effect showing most of the variation in the 2014 start, peak, finish, or duration of flowering of tagged plants was explained by sub-locale and very little was explained by elevation and location (Lake Hazen, Ellesmere Island, Nunavut versus Iqaluit, Baffin Island, Nunavut) where N is the number of tagged plants. Reprinted with permission from The University of Chicago Press.	29
Table 2.4. 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 where N is the number of tagged plants. Reprinted with permission from The University of Chicago Press.	29
Table 2.5. Mean daily maximum, minimum and mean temperatures 5 cm above ground (°C) (18th June - 27th July 2014) at sub-locales at Lake Hazen, Ellesmere Island, Nunavut and Iqaluit, Baffin Island, Nunavut. Reprinted with permission from The University of Chicago Press.	31
Table 3.1. Comparison of number of flowers per population on the date of peak flowering (Table 3.3) and number of tagged plants that produced flowers (30 tagged plants in each population) of <i>Arnica angustifolia</i> (narrow-leaved arnica), <i>Cassiope tetragona</i> (Arctic white heather), and <i>Pedicularis capitata</i> (capitate lousewort) over 3 years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. Reprinted with permission from Ottawa Field-Naturalists' Club.....	44
Table 3.2. Mean monthly temperature from May to September, 2012–2015, compared with 10-year (2001–2010) and 30-year (1981–2010) means at Eureka Weather Station, Ellesmere Island, Nunavut, Canada (Environment Canada, 2016). Reprinted with permission from Ottawa Field-Naturalists' Club.	44
Table 3.3. Dates for start, peak, and finish of flowering of <i>Arnica angustifolia</i> (narrow-leaved arnica), <i>Cassiope tetragona</i> (Arctic white heather) and <i>Pedicularis capitata</i> (capitate lousewort) over 3 years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. Reprinted with permission from Ottawa Field-Naturalists' Club.....	47

Table 4.1. Standard least squares models showing how much of the <i>Dryas integrifolia</i> and <i>Saxifraga oppositifolia</i> peak flower and fruit day of year is explained by year and April, May, June, and July mean temperatures. Reprinted with permission from Canadian Science Publishing.....	61
Table 4.2. 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 α = 0.05, and pale grey = significant at α = 0.10). Reprinted with permission from Canadian Science Publishing.	63
Table 5.1. Mean, standard deviation, minimum, maximum and range of flowering day of year (DOY) over the past 120 years (1896-2015) and classification of early-, mid-summer- or late-flowering of 23 plant species as determined from herbarium specimens, photographs and field observations collected from across Nunavut, Canada.	84
Table 5.2. Standard least squares mixed model results at different spatial scales with flowering DOY as the response variable, species as a random effect and May, June, July and August mean temperatures as fixed effects, showing June mean temperature generally has the greatest influence on the time of flowering and models have better fit at finer-grained spatial scales.	86
Table 5.3. Standard least squares mixed model results at different spatial scales with dispersing seed DOY as the response variable, species as a random effect and May, June, July and August mean temperatures as fixed effects, showing July mean temperature generally has the greatest influence on the time of seed dispersal and models have better fit at finer-grained spatial scales.	87

Table 5.4. Correlation of monthly mean or annual mean temperatures ($^{\circ}\text{C}$) versus year (1946-2015) for the 11 long-term weather stations in Nunavut, Canada where β is the rate of change in monthly temperature in days/yr. Grey shading indicates a significant warming trend (dark grey = $R^2 \geq 0.1$ and pale grey = $R^2 < 0.1$). . 91

Table 6.1. Linear regression of species' peak flowering time day of year (DOY) versus June mean temperature along an elevational gradient, where β is the flowering time temperature-sensitivity (days/ $^{\circ}\text{C}$) with a negative β indicating earlier flowering with warmer June mean temperatures. 104

Table 6.2. Linear regression of species' seed dispersal time day of year (DOY) versus July mean temperature along an elevational gradient, where β is the seed dispersal time temperature-sensitivity (days/ $^{\circ}\text{C}$), a negative β indicates earlier seed dispersal with warmer July mean temperatures. 105

Table 6.3. Tukey-Kramer HSD ANOVA test for significant differences in mean growing degree days (GDD) required to reach peak flower between the coldest, intermediate (int,) and warmest sites (indicated by different letters) for each species and for all species combined..... 107

Table 6.4. Maximum, minimum, range and mean growing degree days (GDD) required by a species to reach peak flower. 108

List of Figures

Figure 1.1. Map of the Canadian Arctic.	2
Figure 2.1. Location of Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada (81.82°N, 71.36°W) and Iqaluit, Baffin Island, Nunavut (63.75°N, 68.55°W). Reprinted with permission from The University of Chicago Press.	20
Figure 2.2. Comparison of mean start, peak, finish 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 days 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 ($t = 2.06$, $P = 0.918$, $N = 13$) and D) flowering duration was significantly longer at Iqaluit than at Lake Hazen ($t = 2.06$, $P = 0.038$, $N = 13$, 6 days longer at Iqaluit). The box plots show the quartiles and mean (dotted line) flowering day of year (DOY) and flowering duration. Reprinted with permission from The University of Chicago Press.	27
Figure 2.3. 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 ($R^2 = 0.70$, $\rho = 0.84$, $P < 0.0001$, $N = 17$). Reprinted with permission from The University of Chicago Press.	30

Figure 3.1. Flower progression of (A) *Arnica angustifolia* (narrow-leaved arnica) (B) *Cassiope tetragona* (Arctic white heather) and (C) *Pedicularis capitata* (capitate lousewort) at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada, showing flower(s) in bud (Ai, Bi and ii, and Ci), open flowers (Aii and iii, Biii and iv, and Cii and iii) and finish of flowering (Aiv and v, Bv and Civ). Photos: Zoe A. Panchen (panels A and C), Carly Cassey (panel B). Reprinted with permission from Ottawa Field-Naturalists' Club..... 42

Figure 3.2. *Arnica angustifolia* (narrow-leaved arnica) population on a southwest facing stream bank, southeast of McGill Mountain, Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. Over 100 flowers are visible in the 2013 photograph (A) and just 20 flowers (marked with white plastic plant tags) in 2014 (B). Both photos are of the same site taken from approximately the same position and angle but B is at a lower magnification than A. The patch of vegetation at the top right of A is on the centre skyline in B and the dip in the centre skyline in A is on the left in B. Photos: Zoe A. Panchen. Reprinted with permission from Ottawa Field-Naturalists' Club. . 45

Figure 3.3. *Cassiope tetragona* (Arctic white heather) in a northeast facing gully on McGill Mountain, Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada with over 300 flowers in 2013 (A) and with just three flowers in 2014 but over 100 flowers/fruits from 2013 still visible (B). Photos: Zoe A. Panchen. Reprinted with permission from Ottawa Field-Naturalists' Club. 46

Figure 4.1. 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. Reprinted with permission from Canadian Science Publishing. 55

Figure 4.2. (A) Mature fruit stage of *Saxifraga oppositifolia* and (B) twisted fruit stage of *Dryas integrifolia*. Reprinted with permission from Canadian Science Publishing..... 57

Figure 4.3. (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 ($R^2 = 0.03$, $P = 0.4769$, $N = 17$). Reprinted with permission from Canadian Science Publishing..... 62

Figure 4.4. 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 4.2). Reprinted with permission from Canadian Science Publishing. 64

Figure 4.5. Average (1989–2014) monthly mean minimum, monthly mean maximum, and monthly mean temperatures at Tanquary Fiord, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada (Table A2.2). Reprinted with permission from Canadian Science Publishing.....	65
Figure 5.1. Locations of (a) flowering and (b) seed dispersing collections (1946-2015) colour coded by the assigned weather station for each location.	78
Figure 5.2. Years in which collections were made of flowering and dispersing seed herbarium specimens, photographs and field observations from the Nunavut mainland and Nunavut archipelago regions, Nunavut archipelago islands, and the Lake Hazen and Iqaluit locales. The black markers indicate years in which one or more collections were made.	79
Figure 5.3. (a) Range of flower day of year (DOY) of each species grouped as early- (blue), mid-summer- (green), and late-flowering (orange) species, (b) range of early-, mid-summer-, and late-flowering species with mean range of flowering DOY (dotted line) of 65.5, 56.9 and 67.7 days respectively and (c) flowering time temperature-sensitivity (β) (days/ $^{\circ}$ C) of early-, mid-summer-, and late-flowering species with mean β (dotted line) of -1.71, -2.10 and -1.67 days/ $^{\circ}$ C respectively.....	85
Figure 5.4. Species' flowering time temperature-sensitivity (β) at different spatial scales in Nunavut, Canada. Significant sensitivity is to the right of the dashed vertical line (Table A3.2).	88
Figure 5.5. Standard least squares mixed model with (a) flowering DOY (Day of Year) and (b) dispersing seed DOY as the response variable, species as a random	

effect and year as a fixed effect across 23 species (a) and 20 species (b) in Nunavut where β is the days/decade change in flowering or seed dispersal time and trend line represents the best fit for each species. 89

Figure 5.6. June mean temperatures since 1946 with regime shift trend line for the 11 long-term weather stations in Nunavut, Canada (Table A3.2). Baker Lake, Cambridge Bay and Coral Harbour have experienced continually rising temperatures in June since 1946; Alert, Eureka, Isachsen and Resolute have experienced a regime shift from a cooling period to a warming period in June; Clyde, Hall Beach and Iqaluit have experienced no significant warming in June since 1946; and Pond Inlet has experienced a regime shift from a steady temperature to a warming period in June. 92

Figure 6.1. Species' peak flowering time (day of year [DOY]) sensitivity to June mean temperature (β) showing how much earlier the species flowers with warmer June mean temperatures (Table 6.1). The size of the points on the graphs is proportional to the number of plants that peak flowered on the DOY and June mean temperature co-ordinate and grey shading indicates the 95% confidence limit. 104

Figure 6.2. Species' seed dispersal time (day of year [DOY]) sensitivity to July mean temperature (β) showing how much earlier the species disperses seed with warmer July mean temperatures (Table 6.2). The size of the points on the graphs are proportional to the number of plants that peak flowered on the DOY and July mean temperature co-ordinate and the grey shading indicates the 95% confidence limit. 105

Figure 6.3. Growing degree days (GDD) for each elevation (1st June - 31st July 2015) (A).

The inset graphs (B) illustrate an expected temperature gradient along an elevational gradient and the actual temperature gradient observed at Lake Hazen. The warmest site is at the mid elevation because Lake Hazen is ice covered until the end of July (Surdu et al. 2015) and hence sites closer to the lake are colder than those at the middle elevation while sites at the highest elevations are colder than those at middle elevations. 106

Figure 6.4. Growing degree days (GDD) required to reach peak flower of all seven species (Table 6.3) at the coldest, intermediate and warmest sites, showing that plants at the coldest site require significantly fewer GDD to reach peak flower than plants at the intermediate and warmest sites..... 107

List of Appendices

Table A1.1 Mean start, peak and finish of flowering day of year (DOY) and duration of flowering in 2013 of species populations across sub-locales (Iqaluit: 1=Apex, 2=Iqaluit city, 3=Sylvia Grinnell Territorial Park, 4=Road to Nowhere; Lake Hazen: 5=Camp Hazen, 6=Skeleton Lake, 7=plateau below and south east of McGill Mountain and 8=north east upper slopes of McGill Mountain) at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut and Iqaluit, Baffin Island, Nunavut..... 141

Table A1.2 Mean start, peak, finish of flowering day of year (DOY) and duration of flowering in 2014 of N tagged plants across sub-locales (Iqaluit: 1=Apex, 2=Iqaluit city, 3=Sylvia Grinnell Territorial Park, 4=Road to Nowhere; Lake Hazen: 5=Camp Hazen, 6=Skeleton Lake, 7=plateau south east of McGill Mountain and 8=north east upper slopes of McGill Mountain) at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut and Iqaluit, Baffin Island, Nunavut.....143

Figure A1.1 Comparison of order of peak flowering by species in 2013 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 ($R^2 = 0.42$, $\rho = 0.64$, $P < 0.002$, $N = 21$).....144

Figure A1.2 Comparison of order start flowering (A) and finish flowering (B) by species in 2014 at Lake Hazen, Ellesmere Island, Nunavut and Iqaluit, Baffin Island, Nunavut showing that the order of start and finish flowering is consistent between Iqaluit and Lake Hazen (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).....	145
Table A2.1. Tanquary Fiord, Quttinirpaaq National Park, Nunavut, Canada monthly temperature reconstruction formulas and the correlation of 1989-2014 Tanquary Fiord monthly temperatures and 1989-2014 Eureka Environment Canada Weather Station, Nunavut, Canada monthly temperatures.....	147
Table A2.2. Tanquary Fiord, Quttinirpaaq National Park, Nunavut, Canada 1989-2014 mean, standard deviation, minimum, maximum and range of annual and monthly mean minimum, monthly mean maximum and monthly mean temperatures.....	148
Table A3.1. Sources of flowering time and seed dispersal time data. The physical herbarium specimens were examined at CAN, DAO, TRTE and Tanquary Fiord herbaria and digitised specimens were examined from ACAD, QFA and ALA.	149
Table A3.2. Linear regressions for each species at each spatial scale with flowering DOY as the response variable and June mean temperature as the explanatory variable where temperature-sensitivity is β in days/ $^{\circ}\text{C}$ and grey shading indicates significant earlier flowering with warmer June mean temperature ($P < 0.05$) (dark grey = $R^2 \geq 0.1$ and pale grey, a weak trend = $R^2 < 0.1$).....	150
Table A3.3. Mean monthly temperature regime shift analysis for annual, June and July mean temperatures for the 11 long-term weather stations in Nunavut using a nonlinear least squares models where break pt. yr. is the estimated year of the regime shift and β is the rate of change in temperature before and after the	

regime shift. Blue shading indicates a significant cooling trend (negative β)
and orange shading indicates a significant warming trend (positive β).....152

1 Chapter: Introduction

The Arctic is predicted to experience unprecedented climate change with temperatures rising dramatically, the beginnings of which are already being felt throughout the Arctic (McBean, 2004; Furgal and Prowse, 2007; AMAP, 2011; Stocker et al., 2013). Phenology is the timing of life cycle events such as flowering and fruiting and is strongly influenced by seasonal temperatures (Rathcke and Lacey, 1985; Fitter et al., 1995; Panchen et al., 2012). In temperate regions, there is a growing body of research on plant responses to climate change. However, the underlying factors controlling Arctic climate and Arctic climatic change differ from temperate regions. Thus, with temperature increases anticipated in the Arctic, the question arises as to how Arctic plants will respond to contemporary climate change. This thesis, therefore, focuses on Arctic flowering and fruiting phenology and its sensitivity to climate change in Nunavut, Canada.

The southern limit of the Arctic is varying defined as the (i) Arctic Circle (66.55°N), (ii) latitude at which the sun is above the horizon 24 hours/day in mid-summer (66.55°N), (iii) tree line, (iv) southernmost limit of continuous permafrost, (v) 10°C isotherm of the warmest month of the year, (vi) net radiation balance of < 62.7 KJ/cm²/year or (vii) Nordenskjöld line defined by $V < 9^{\circ}\text{C} - 0.1K$ where V is the warmest and K is the coldest month (Pielou, 1994; Przybylak, 2003). For the purpose of this thesis, the definition used is the tree line, coinciding approximately with the southernmost limit of continuous permafrost in Nunavut.

Nunavut, a territory of 2.1 million km², is almost entirely Arctic in nature (Figure 1.1). The tree line and limits of continuous permafrost dip well south of the Arctic Circle

around Hudson Bay. Nunavut is bound on the east by Baffin Bay and the narrow straits between Ellesmere Island and Greenland and on the west by longitude 110°W but extends further west on southern Victoria Island and the mainland. Baffin Island is the largest island of the Canadian Arctic Archipelago, occupying one-third of the archipelago's land area. Ellesmere and Victoria Islands are less than half the size of Baffin Island (Edlund and Alt, 1989; Woo and Ohmura, 1997; Przybylak, 2003).

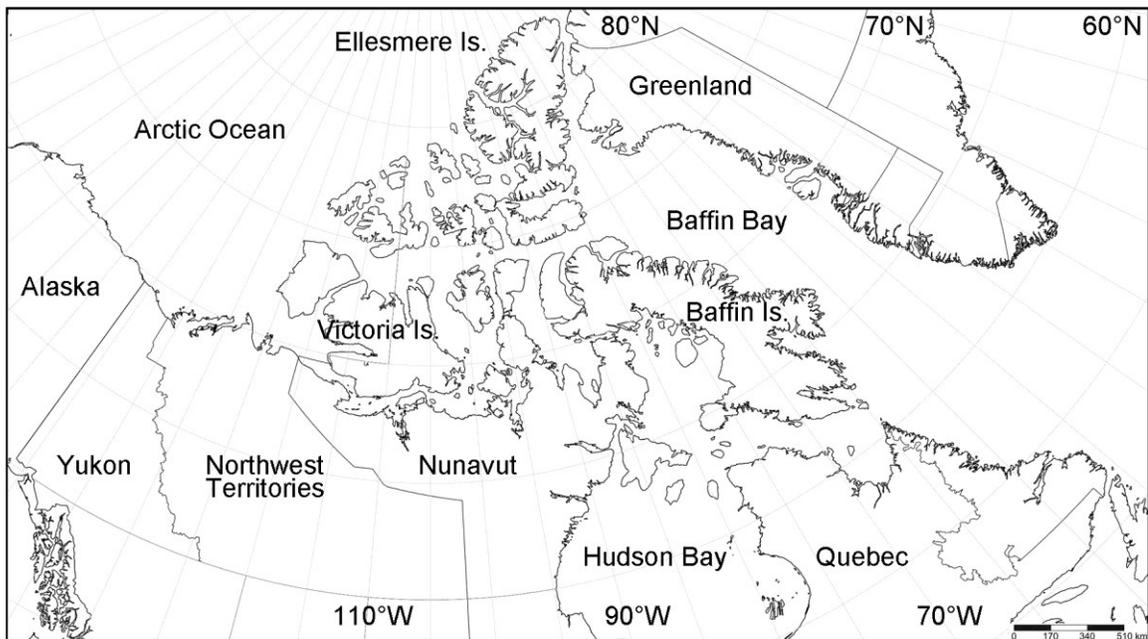


Figure 1.1. Map of the Canadian Arctic.

Given that temperature has a major influence on plant phenology, for this thesis it is necessary to understand the Arctic's climate and how the Arctic climate will change. Thus, this chapter first discusses the underlying factors controlling the Arctic climate and how those factors drive Arctic climate change with a particular focus on the Canadian Arctic and temperature. The chapter then discusses temperate plant reproductive phenology in the changing climate and finally concludes with a discussion on what is

currently known about Arctic plant reproductive phenology in relation to changes in temperature.

1.1 Arctic climate and climate change in the Canadian Arctic

Climate is the long-term summary of weather conditions (Barry and Carleton, 2001). Climate includes inter-annual and cyclic variations but long-term trends are of greater interest in understanding climate change (Davis et al., 2015; Baker et al., 2016). Arctic meteorological recording has waxed and waned with Arctic nations' economic fortunes and perceived importance of sovereignty (Przybylak, 2003; Holopainen et al., 2013). The sparse distribution of Arctic weather stations, the often discontinuous historic weather data and the coastal location of most weather stations has led to challenges in describing the Arctic climate accurately and analysing trends (Edlund and Alt, 1989; Hertzman, 1997; Woo and Ohmura, 1997; Barry and Carleton, 2001; Atkinson and Gajewski, 2002; Przybylak, 2003). Although there are pockets of earlier data (Burn and Kokelj, 2009; Burn and Zhang, 2009), meteorological recording in the Canadian Arctic started in earnest after the Second World War and was further expanded in the late 1950s with the establishment of the Distant Early Warning (DEW) Line (Przybylak, 2003; Environment Canada, 2016).

The Arctic climate is influenced by global and local climate forces (Edlund and Alt, 1989; Hare, 1997). Air circulation and ocean currents are the principal global climate forces, bringing sensible and latent heat from tropical and temperate regions and returning colder air and water southwards, thus moderating the global climate (Hare, 1997). Major local factors influencing the Arctic climate are solar radiation and the cryosphere (Edlund and Alt, 1989; Hare, 1997). The oblique angle of the sun's radiation

and longer distance it travels through the atmosphere to reach the Arctic result in less radiation being received per unit surface area in the Arctic than further south. The sun's absence in mid-winter to 24 hours/day presence in summer is also a strong factor in the amount of energy the Arctic receives (Przybylak, 2003). The cryosphere, the permanent or seasonally frozen components of the Earth's land and sea surface, creates a temporary or permanent barrier between air circulation and the water and land (AMAP, 2012a). The albedo or solar reflectance of the cryosphere also reflects a large proportion of the radiation from the sun (AMAP, 2012a).

Globally, temperatures have risen twice as much in the last 60 years (1951-2012) than in the prior 60 years (1901-1960) (Stocker et al., 2013). The changes in the Arctic have been even greater. Temperatures have risen four times as much in the last 40 years (1966-2003) than the last century (1900-2003) (0.4 versus 0.09°C/decade) (McBean, 2004) and since 1980 the rate of temperature increase in the Arctic has been double that of temperate regions (AMAP, 2012b; Hartmann et al., 2013). Canadian Arctic temperatures have risen 2-3°C over the last 50 years (Maxwell, 1997; Przybylak, 2003; Furgal and Prowse, 2007). Since 1900, the Arctic has experienced both warming and cooling periods with a warming trend from 1900 to 1940s, then a cooling trend from the late 1940s to the 1960s and since the 1970s another warming trend (Overpeck et al., 1997; Przybylak, 2003; McBean, 2004; AMAP, 2012b; Hartmann et al., 2013). In general, the most significant Arctic temperature changes have been in the autumn (Przybylak, 2003; AMAP, 2012b). The warming trend is almost double at higher Arctic latitudes than lower ones, 0.4°C/decade versus 0.25°C/decade (McBean, 2004).

The factor that will perhaps have the greatest impact on climate change in the Canadian Arctic is the cryosphere (Furgal and Prowse, 2007). The extent and thickness of sea ice has reduced since the 1970s by 10-15% and 40% respectively (McBean, 2004; Furgal and Prowse, 2007; AMAP, 2012a; Stocker et al., 2013). Summer sea ice cover is now at record lows with the area covered one-third less than in 1979-2000 (AMAP, 2011). The proportion of first-year ice has increased while multi-year ice has decreased (McBean, 2004; Furgal and Prowse, 2007; AMAP, 2012a). More open water results in a lower albedo and more solar heat absorbed by Arctic waters. The warmer water radiates the increased heat back into the atmosphere delaying the formation of ice until later in the season and so further reducing the extent and thickness of multiyear sea ice the following year. Hence this positive feedback loop in the Arctic is exacerbating climate change (McBean, 2004; AMAP, 2012a).

The number of days with snow cover in the Arctic has declined by up to two weeks from 1972/3 to 2008/9 (AMAP, 2012a). Arctic-wide, most of that reduction is in spring but in the Canadian Arctic Archipelago it is more pronounced in the autumn. Ice on lakes and rivers is breaking up earlier and freezing later, resulting in 33 fewer days of ice cover on lakes in the high Canadian Arctic (1985- 2004) (AMAP, 2012a). Arctic glaciers and icecaps are retreating and ice shelves are breaking up (Mueller et al., 2003; Copland et al., 2007; Stocker et al., 2013). The Canadian Arctic is one of the largest contributors to Arctic ice loss (AMAP, 2012a; Sharp et al., 2014). With snow melting earlier and settling later, lakes and rivers melting earlier and freezing later, and glaciers and ice caps receding, there is less albedo and more heat absorption by the land and so there is a

similar positive feedback loop on the land as on the ocean (McBean, 2004; Furgal and Prowse, 2007; AMAP, 2012b).

Contemporary climate change started later in the Arctic than in temperate regions because of the extra energy required to overcome the latent heat effects of the cryosphere (Przybylak, 2003). There has been a slowdown in the rate of climate change in the last 15 years (Stocker et al., 2013). However, warming trends are sensitive to the range of years included, particularly for short time periods, and hence this apparent slow-down should be treated with caution (Stocker et al., 2013; Baker et al., 2016).

It is worth mentioning that 3.5 million years ago when the world was 2-3°C warmer than today, the Arctic was 14-22°C warmer (Rybczynski et al., 2013), showing how sensitive the Arctic region is to climate change. Climate change scenarios based on the Intergovernmental Panel on Climate Change (IPCC) 2013 Fifth Assessment Report (AR5) models are predicting that in the Canadian Arctic temperatures will rise by 4-5°C by 2050 (Fenech, 2013).

In summary, the Arctic climate is driven by external factors of air and ocean circulation bringing warmth and moisture to the Arctic and local factors of solar radiation, and albedo, latent heat and insulation of the cryosphere. Changes in the cryosphere caused by climate change are likely to accelerate and accentuate climate change in the Arctic.

1.2 Plant reproductive phenology in a changing climate

Phenological events have been recorded by diarists, naturalists and botanists over the last century or more in Europe and North America (Schwartz, 1994; Menzel, 2000; Miller-Rushing and Primack, 2008; Bock et al., 2014). Herbarium specimens and dated

photographs provide other historic records of flowering and fruiting phenology (Miller-Rushing et al., 2006; Davis et al., 2015). Combined with historical weather records, these historic phenology records are now being used to great effect for phenology-climate change studies (Menzel and Fabian, 1999; Miller-Rushing and Primack, 2008; Bock et al., 2014). Two measures are typically used to quantify plant phenological responses to climate change. The first is phenological change over time measured in days/decade, where a negative measure implies an earlier or advancing phenological event over time. However, this measure is susceptible to the range of years used due to inter-annual variations in temperature (Iler et al., 2013a; Davis et al., 2015; Baker et al., 2016). The second is phenological change with temperature measured in days/°C, which is a measure of the sensitivity of the plant's phenology to temperature, where a negative measure implies earlier or advancing phenology with warming temperatures. However, this measure can only be used to predict how responsive a species might be to climate change (Calinger et al., 2013; Davis et al., 2015). The sum of temperature above a threshold temperature on consecutive days influences timing of phenological events, that is the cumulative effect of temperature or growing degree days (Kimball et al., 2014). Most phenology-climate change research typically uses monthly mean temperatures as an approximation for the cumulative effect of temperature on the timing of plant phenological events.

Rising temperatures of climate change are causing many plant species to flower earlier in temperate regions (Fitter et al., 1995; Primack et al., 2004; Miller-Rushing and Primack, 2008; Gallagher et al., 2009; Rumpff et al., 2010; Panchen et al., 2012; Bock et al., 2014). The greatest changes in flowering time are being observed in early-flowering

species (Fitter et al., 1995; Menzel and Fabian, 1999; Bock et al., 2014) and are likely due to spring temperatures rising more than summer and autumn temperatures in temperate regions (Menne et al., 2010; Stocker et al., 2013). Warmer temperatures also result in shorter flowering duration (Bock et al., 2014). In temperate North America, flowering phenological responses are in the range of -0.3 to -8.0 days/decade and -0.5 to -5.0 days/°C (Bradley et al., 1999; Abu-Asab et al., 2001; Cayan et al., 2001; Primack et al., 2004; Ledneva et al., 2004; Wolfe et al., 2005; Lavoie and Lachance, 2006; Miller-Rushing and Primack, 2008; Neil et al., 2010; Anderson et al., 2012; Panchen et al., 2012; Calinger et al., 2013; Iler et al., 2013a; CaraDonna et al., 2014; Davis et al., 2015). Temperatures in the month or months just prior to flowering have the strongest influence on the timing of flowering (Fitter et al., 1995; Cayan et al., 2001; Chmielewski and Rötzer, 2001; Primack et al., 2004; Menzel et al., 2006; Miller-Rushing and Primack, 2008; Robbirt et al., 2010; Panchen et al., 2012). Phenological sensitivity to temperature varies among species, even closely related species (Fitter et al., 1995; Miller-Rushing and Primack, 2008; Panchen et al., 2012). Woody plants are more sensitive than herbaceous plants, while non-native species to North America are more sensitive than native North America species (Fitter et al., 1995; Abu-Asab et al., 2001; Miller-Rushing and Primack, 2008; Willis et al., 2010; Panchen et al., 2012). Phenological temperature-sensitivity does show some phylogenetic patterns (Willis et al., 2008; Davis et al., 2010; Davies et al., 2013; Lessard-Therrien et al., 2013; Mazer et al., 2013; Panchen et al., 2015).

Climate change implications for fruiting phenological events have been less well studied (Gallinat et al., 2015) but there has been greater change in spring phenological events than autumn phenological events in temperate regions (Menzel, 2000).

1.3 Arctic plant reproductive phenology and temperature

Arctic plants have a number of reproductive phenological strategies to maximise reproductive success in the short, cold Arctic growing season with temperature having been a key driver in the evolution of Arctic plants (Bliss, 1971). Early-flowering species tend to be out-breeders, less successful as selfers and have high seed abortion rates, while late-flowering species tend to be more successful as selfers, apomictic, viviparous and have low seed abortion rates (Stenström and Molau, 1992; Eriksen et al., 1993; Molau, 1993a; b). These strategies are referred to as ‘pollen risk’ and ‘seed risk’, respectively, where the seed output of both are similar but early-flowering species (pollen risk) have a low steady output every year, while late-flowering species (seed risk) have high seed output but only in favourable (warm and long) years (Molau, 1993a). Hence, with respect to the seed bank, climate change might favour late-flowering species (Molau, 1993a). Early-flowering species tend to be shrub and cushion species and require fewer growing degree days to flower while late-flowering species tend to be graminoid and herbaceous species requiring more growing degree days (Thórhallsdóttir, 1998; Molau et al., 2005). Early-flowering species also tend to have distribution ranges to higher elevations than late-flowering species (Molau et al., 2005). Because of the short growing season, most Arctic species pre-form their flower buds the year or years prior to flowering, early-flowering species have pre-formed flower buds at an advanced stage of development while late-flowering species have less well developed pre-formed flower buds (Sørensen, 1941; Molau et al., 2005). Temperatures in May or June, i.e. soon after snowmelt (Eriksen et al., 1993; Levesque et al., 1997; Molau, 1997), or temperatures five weeks before flowering (Thórhallsdóttir, 1998) have a strong influence on the timing of

flowering. Late-flowering species are more sensitive to temperature than early- or mid-flowering species (Molau et al., 2005; Iler et al., 2013a). Warmer temperatures also reduce the duration of flowering (Ellebjerg et al., 2008; Høye et al., 2013) and could lead to more reproductive success for seed risk plants (Molau, 1993a; Molau et al., 2005). In contrast to temperate regions, where the growing season is lengthening predominantly at the start of the season (Menzel and Fabian, 1999), the Arctic growing season is lengthening predominantly at the end of the growing season likely because of the effects of the cryosphere. Temperatures at the end of the growing season are rising, while those at the start of the growing season are rising less or not at all (Blinova and Chmielewski, 2015).

Over the last 10 to 15 years the body of knowledge on plant phenology in relation to climate changes has risen exponentially. However, the same cannot be said for the Arctic (Høye et al., 2007b; Holopainen et al., 2013), likely due to the remote nature of the region and hence logistical challenges of monitoring and collecting phenological data. Long-term phenology records are few and far between in the Arctic, particularly in Nunavut (Callaghan, 2005; Høye et al., 2007b; Holopainen et al., 2013). There have, however, been a number of *in-situ* experimental warming studies in the Arctic, many of which were conducted as part of the International Tundra Experiment (ITEX) (Henry and Molau, 1997). Not surprisingly, the experimental warming studies show that flowering times of many Arctic plant species were earlier with warmer temperatures (Wookey et al., 1993; Alatalo and Molau, 1995; Molau, 1997; Welker et al., 1997; Arft et al., 1999; Stenström and Jónsdóttir, 2004; Oberbauer et al., 2013; Bjorkman et al., 2015; Khorsand Rosa et al., 2015). There was a greater advance in flowering time with warmer

temperatures for male than for female flowers in a number of dioecious and monoecious species (Alatalo and Molau, 1995; Jones et al., 1997; Stenström and Jónsdóttir, 2004). Graminoid and herbaceous species were more responsive to increased temperatures than woody plants (Arft et al., 1999; Kremers et al., 2015) which is the opposite of temperate region observations, although studies in Greenland indicate that shrubs are more responsive than other plant types (Ellebjerg et al., 2008). Air temperature is a better predictor of phenology than soil temperature (Khorsand Rosa et al., 2015). The phenological response to experimental warming lessens over time (Oberbauer et al., 2013; Kremers et al., 2015). The few long-term phenology studies concur with the experimental warming studies in that warmer temperatures result in earlier flowering (Høye et al., 2007a; Cadieux et al., 2008; Ellebjerg et al., 2008; Barrett et al., 2015).

Few experimental warming studies and no long-term phenology studies have observed earlier fruiting phenology with warmer temperatures (Ellebjerg et al., 2008; Bjorkman et al., 2015). However, a number of experimental warming studies have observed increased reproductive output with warmer temperatures including increased seed set, seed weight, fruit set, fruit weight and seed viability (Wookey et al., 1993; Alatalo and Molau, 1995; Levesque et al., 1997; Molau, 1997; Welker et al., 1997; Arft et al., 1999; Naoya, 1999; Stenström, 1999; Klady et al., 2011).

The flowering and fruiting phenology of a few species did not respond to warmer temperatures (Wookey et al., 1993; Jones et al., 1997; Stenström et al., 1997; Totland and Alatalo, 2002) perhaps because, for these species, the reproductive phenology is influenced by other factors such as photoperiod or soil moisture (Holway and Ward,

1965; Woodley and Svoboda, 1994; Keller and Körner, 2003; Ranjitkar et al., 2013; Wolkovich et al., 2013).

There is evidence that the snow-free date influences time of flowering of Arctic plants (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., 2013b; Bjorkman et al., 2015). However, there are exceptions, particularly where there is minimal snow accumulation over winter (Thórhallsdóttir, 1998; Molau et al., 2005; Ellebjerg et al., 2008; Bienau et al., 2015). In fact, Thórhallsdóttir (1998), Borner et al. (2008), Petraglia et al. (2014) and Barrett et al. (2015) go as far as to state that air temperature, not snowmelt date, is likely the underlying or stronger factor controlling Arctic flowering phenology, while Legault and Cusa (2015) suggest snowmelt date and air temperature together influence reproductive phenology. Under current climate change, warmer temperatures and less snow cover (Callaghan, 2005) is exposing plants to an increased risk of frost damage in early spring and hence cold exposure will also be a factor impacting Arctic plant flowering and reproduction (Inouye and McGuire, 1991; Høye et al., 2007a; Ellebjerg et al., 2008; Inouye, 2008; Semenchuk et al., 2013; Wheeler et al., 2015).

1.4 Thesis Overview

The main objectives of this thesis are to first study the reproductive phenology of Arctic plant species in Nunavut and how phenology differs across the territory; second, to assess how the reproductive phenology of Nunavut plant species has changed under contemporary climate change; third, to assess reproductive phenology temperature-sensitivity of Arctic plant species as a predictor of their responses to climate change; and

fourth to determine climate change, specifically temperature changes, in Nunavut. A principal hypothesis of this thesis was that Arctic plant phenological events occurring later in the Arctic growing season will advance more than early-season Arctic plant phenological events because, in contrast to temperate regions, the greatest climatic changes in the Arctic are currently occurring in autumn and winter.

Arctic plant reproductive phenology has been understudied (Thórhallsdóttir, 1998; Høye et al., 2007b). This is particularly true in Nunavut where studies at Alexandra Fiord, Ellesmere Island by Woodley and Svoboda (1994), Lavesque et al. (1997) and Bjorkman et al. (2015) are some of the few studies on Nunavut reproductive phenology. Understanding the Arctic plant phenology in Nunavut should, therefore, be a prerequisite to studying the impacts of climate change on Nunavut Arctic plants. The Arctic lands in Nunavut cover the entire spectrum of Arctic latitudes from the tree line at 60°N by Hudson Bay to the very northern limits of Arctic land at 83°N on northern Ellesmere Island. Based on common garden studies (Clausen et al., 1941; van Dijk et al., 1997; Weber and Schmid, 1998; Olsson and Ågren, 2002; Wagner and Simons, 2009; Bjorkman et al., 2015), it is possible that there are differences in the phenology of conspecifics across Nunavut. Hence, Chapter 2 is a baseline study of the timing and duration of flowering of common Nunavut Arctic plant species at a mid-Arctic location, Iqaluit, Baffin Island (63.75°N, 68.55°W) and a High Arctic location, Lake Hazen, Ellesmere Island (81.82°N, 71.36°W), and compares the timing and duration of flowering between these two locations. These two locations were chosen as they have been reasonably well studied botanically and were logistically feasible (Savile, 1964; Kevan, 1972; Porsild and Cody, 1980; Gould, 1985; Soper and Powell, 1985; Healy and

Gillespie, 2004; Aiken et al., 2011). Hence, this chapter serves as a historical and current reference to support subsequent chapters.

The majority of Arctic plants pre-form their flower buds the year or years prior to flowering (Sørensen, 1941). Contemporary climate change is exhibiting extreme weather events and years with extreme weather contrasts (Easterling et al., 2000a; b; Semenchuk et al., 2013; Stocker et al., 2013). Chapter 3 is a natural history of flower abundance at Lake Hazen over three years of observations with extreme contrasts in weather (2013-2015) and highlights the flowering phenology and reproductive success implications in a changing climate.

Historic phenology and weather records can be used to assess how plant phenology has changed due to climate change in the recent past and to predict how plants will respond phenologically to continued climate change. Chapter 4 uses one of the very few long-term phenology records in Nunavut to address the questions (i) How has flowering and fruiting phenology changed in the last 20 years (1994-2014)?, (ii) How sensitive is Arctic plant reproductive phenology to temperature? and (iii) How have temperatures changed over the last 25 years (1989-2014)? The long-term phenology records are from Tanquary Fiord, Quttinirpaaq National Park, Ellesmere Island (81.4°N, 76.7°W) and use the ITEX protocol. Tanquary Fiord is 100 km southwest of Lake Hazen and experiences a similar climate (Soper and Powell, 1985; Edlund and Alt, 1989; Thompson, 1994).

Chapter 5 uses herbarium specimens, field observations and dated photographs collected from across Nunavut over the last 120 years (1896-2015) to predict flowering and seed dispersal time sensitivity to climate change, assess the changes in flowering and

seed dispersal times over the 120-year period and assess changes in temperature since 1946. This chapter further compares differences in flowering phenology sensitivity to temperature across the region. More broadly, Chapter 5 serves as a proof-of-concept to assess whether phenology-climate change studies using historic data can be conducted at large spatial scales.

Given the scarcity of Arctic phenological records, an alternative approach to assess plant phenological responses to climate change is to substitute space for time. An elevational gradient, with its associated temperature gradient, can be used as a proxy for climate change. Chapter 6, therefore, makes use of the elevational gradient at Lake Hazen to predict the phenological temperature-sensitivity of seven Arctic plant species.

2 Chapter: Canadian Arctic Archipelago conspecifics flower earlier in the High Arctic than the mid-Arctic

2.1 Abstract

The Canadian Arctic Archipelago is experiencing unprecedented climate change with temperatures rising at a rate twice the global average. The rapidly rising temperatures will likely impact plant phenology dramatically. The Canadian Arctic Archipelago is remote and difficult to reach, with few insights into the phenology of its plants. Baseline information about Arctic plant flowering times and how they vary across the Canadian Arctic Archipelago is needed to facilitate studies on the impacts of climate change on Arctic plant phenology. I recorded flowering times of 26 species, from 12 families, common to a High Arctic (82°N) and mid-Arctic (64°N) location in Nunavut, Canada in 2013 and 2014. I compared differences in flowering times and flower abundance between the two locations and identified factors that might explain the differences. Species flowered at the same time or earlier and for a shorter duration at the High Arctic compared to the mid-Arctic location. Different sub-locales at a location explained more of the variation in flowering time than 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 plants at the High Arctic location. Relative order of species' flowering was consistent between the mid- and High Arctic locations, and between years. 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 the mid-Arctic location and that flowering time for a species is influenced by cumulative temperatures above a threshold. My results suggest

that plants at the northern location might be evolutionarily adapted to the shorter growing season and that plants have phenotypic plasticity across sub-locales.

This chapter is reprinted with permission from The University of Chicago Press:
PANCHEN, Z.A. and R. GORELICK. 2016. Canadian Arctic Archipelago conspecifics flower earlier in the High Arctic than the mid-Arctic. *International Journal of Plant Sciences*. DOI 10.1086/687984.

2.2 Introduction

The Canadian Arctic Archipelago is experiencing unprecedented climate change with temperatures rising twice as fast as the global average (Furgal and Prowse, 2007; 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 impacts 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 timing of flowering and fruiting due to climate change have an impact on ecological communities, such as mismatches in the timing of flowering and pollinator arrival/emergence or timing of seed production and 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 vernalisation or a chilling period prior to flowering, a mechanism to prevent flowering during a warm period mid-winter (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 vernalisation, cumulative temperature and threshold temperature requirements. The threshold temperatures for Arctic and alpine plants appear to range between -7°C and $+5^{\circ}\text{C}$ (Kimball et al., 2014; Barrett et al., 2015). Initiation of flowering can also be triggered by a change in day-light 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 is 24 hours of day light per day for the entire growing season ($>63^{\circ}\text{N}$) (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., 2007b; 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 a more southerly latitude, suggesting that this might be due to evolutionary adaptation of the more northerly conspecifics to the harsher environment of a colder, shorter growing season (Clausen et al., 1941; van Dijk et al., 1997; Weber and Schmid, 1998; Olsson and Ågren, 2002; Wagner and Simons, 2009).

I 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 questions (i) What is the timing and duration of flowering of Nunavut Arctic plants?, (ii) What is the difference 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?, and (iv) In relation to the duration of flowering, when do species peak flower?

2.3 Materials and methods

2.3.1 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 (63.75°N, 68.55°W) and the northern location was Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut (81.82°N, 71.36°W) (Figure 2.1). The High Arctic, where Lake Hazen is located, is defined as polar desert (Edlund and Alt, 1989; Przybylak, 2003; Callaghan, 2005). The range of elevations in my study was 4-109 m above sea level (m.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 (79.59°N, 85.56°W) is the closest weather station to Lake Hazen and experiences a similar climate to Lake Hazen (Soper and Powell 1985; Edlund and Alt, 1989; Thompson, 1994) and hence I used Eureka as a proxy to compare the climate between Iqaluit and Lake Hazen. Based on 30-year (1981-2010) means, the growing season in Iqaluit is warmer than Eureka with June-August mean temperature 2.2°C higher at Iqaluit than Eureka and 293.5 more annual degree days above zero at Iqaluit than Eureka but both locations are typically snow free by mid-June (Table 2.1). 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 the 30-year (1981-2010) mean, while the summer of 2014 was similar to the 30-year mean at both Iqaluit and Eureka (Table 2.1).

Both locations were divided into distinct sub-locales: (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 south east of McGill Mountain and the northeast upper slopes of McGill Mountain. Within each sub-locale, areas with established populations of each species were selected prior to start of flowering in 2013. Species were not always present at each sub-locale hence each species was monitored at 1, 2 or 3 sub-locales (Table A1.1 and A1.2). The sub-locales were within a 5 km radius of Iqaluit or the Lake Hazen park warden station.

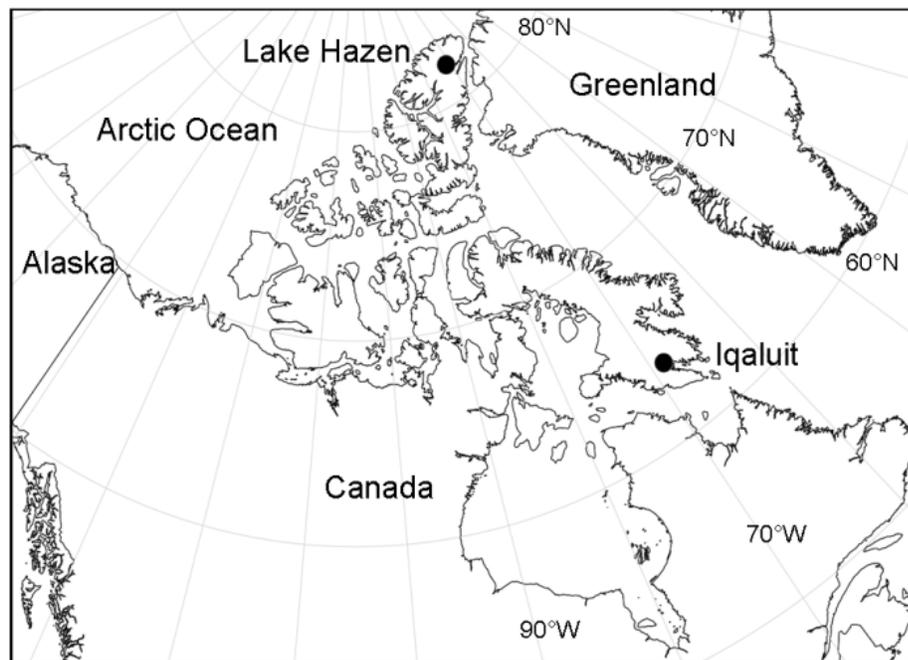


Figure 2.1. Location of Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada (81.82°N, 71.36°W) and Iqaluit, Baffin Island, Nunavut (63.75°N, 68.55°W). Reprinted with permission from The University of Chicago Press.

Table 2.1. Iqaluit and Eureka Environment Canada Weather Stations' 30-year mean, 2013 and 2014 May to August mean temperatures (°C) and 30-year mean annual snowfall, number of days in June with a snow depth greater than or equal to 1cm and annual degree days above zero (Environment Canada 2016). The Eureka weather station is the closest weather station to Lake Hazen, Ellesmere Island, Nunavut and experiences a similar climate (Edlund and Alt 1989; Thompson 1994). Reprinted with permission from The University of Chicago Press.

	30 yr mean		2013		2014	
	Iqaluit	Eureka	Iqaluit	Eureka	Iqaluit	Eureka
May	-4.4	-10.2	-6.7	-12.3	-1.7	-8.5
June	3.6	3.0	2.9	0.5	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
Mean June-Aug.	6.3	4.1	5.9	1.3	6.9	3.7
Annual snowfall (cm)	229.3	60.3				
June days snowdepth \geq 1cm	10.0	8.6				
Annual degree days above 0°C	695.1	401.6				

2.3.2 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 third week of August and at Lake Hazen from the second week of June to last week of July in 2013 and 2014 (Table A1.1 and A1.2). A preliminary study was undertaken in 2013, wherein the date of start, peak and finish of flowering of a species' population at a sub-locale were 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 sub-locale and the number of flowers counted on each tagged plant every site visit. The approach was changed in 2014 to improve statistical power of the analysis. In 2013 it

was only possible to compare timing of flowering between the two locations of all species combined. While, in 2014 each species' timing of flowering between the two locations or between sub-locales could be compared separately. The date of start, peak and finish of flowering of the tagged plants was determined from the tagged plants' flower counts. The aim was to have 30 tagged flowering plants per species at each sub-locale. I also aimed not to bias towards earlier-flowering plants by tagging plants prior to visible buds. However, in some cases there were fewer than 30 plants at a sub-locale or not all the tagged plants flowered, hence the number of flowering tagged plants at a sub-locale in 2014 was not always 30 (Table A1.2). In both years, each sub-locale at the two locations was visited twice per week (i.e. every 3-4 days). For both years, I 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 open when the petals were open, i.e. not in a bud, the petals looked fresh and were not wilted or discoloured, 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 1st January 2013 or 2014. At Lake Hazen in 2013, I did not find *Arnica angustifolia* Vahl in time to record 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 I departed. At Lake Hazen in 2014, *Bistorta vivipara* (L.) Delarbre, *Saxifraga cespitosa* L. and *Saxifraga tricuspidata* Rottb. had not finished flowering by the time I departed. The inflorescence (capitulum holding many small

flowers) of *Arnica angustifolia* was counted as a single flower. Fewer than five plants of the following species had second flowering with only one or two flowers per plant, and therefore I excluded second flowering from their finish of flowering date: *Cardamine bellidifolia* L., *Cerastium arcticum* Lange, *Saxifraga cespitosa*, *Saxifraga oppositifolia* L. and *Silene acaulis* (L.) Jacq.

2.3.3 Temperature

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

2.3.4 Statistical analysis

I used the Student's t difference of means test to analyse the difference between Iqaluit versus 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 duration of flowering separately across species. If the species was monitored at more than one sub-locale in 2013, then the start, peak or finish of flowering DOY used in the Student's t-test was the mean across the sub-locales i.e. the basic sampling unit was at the species level at the location.

I used Welch's difference of means test to analyse the difference between Iqaluit versus Lake Hazen start of flowering DOY of tagged plants for each species separately in 2014. 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.

I used separate linear mixed effect models for each of 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 versus Iqaluit), elevation and sub-locale (nested within location because sub-locals are unique to each location). The mixed effects model used restricted maximum likelihood methods where species was a random effect, location, elevation and sub-locale were fixed effects and each tagged plant was the basic sampling unit.

To determine when peak flowering occurred in relation to duration of flowering, I calculated the mean percent time to peak flowering for each species at Lake Hazen and Iqaluit separately in 2014. That is, I 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. I also used Welch's difference of means test to analyse the difference in peak flower count between Lake Hazen and Iqaluit in 2014 for each species. I tested for skew and kurtosis of the number of flowers open on each site visit for *Cassiope tetragona* (L.) D. Don, *Cerastium arcticum* and *Pedicularis hirsuta* L. at the Road to Nowhere sub-locale. *Bistorta vivipara*, *Saxifraga cespitosa* and *Saxifraga tricuspidata* were not included in the 2014 analysis of finish and duration of flowering, percent time to peak flowering and peak flower count because not all tagged plants had finished flowering. I also excluded *Alopecurus magellanicus* Lam., *Arctagrostis latifolia* (R.Br.) Griseb., and *Eriophorum scheuchzeri* Hoppe from the percent time to peak flowering and peak flower count analysis because I 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 if the order of flowering across species was consistent between Lake Hazen and Iqaluit, I 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 if the order of flowering was consistent between years, I 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, North Carolina, USA).

2.4 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 days longer at Iqaluit); flowering started significantly earlier at Iqaluit than at Lake Hazen ($t = 2.02$, $P = 0.039$, $N = 22$, 8 days 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: $t = 2.06$, $P = 0.918$, $N = 13$) (Figure 2.2). 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 2.2).

More than 77% of start, peak or finish of flowering and 39% of duration of flowering was explained by location, elevation, sub-locale and species (Table 2.3). Sub-locale at a location explained significantly more of the variation in time and duration of flowering in

2014 than the location (Lake Hazen versus Iqaluit) or elevation (Table 2.3). Location and elevation had a greater influence, but still less than sub-locale, on finish of flowering than start, peak or duration of flowering (Table 2.3).

Peak flowering occurred approximately one-third of the way through flowering duration (Table 2.4). The skewness values for the number of flowers open distribution were 1.34 for *Cassiope tetragona*, 0.58 for *Cerastium arcticum* and 0.71 for *Pedicularis hirsuta* indicating a moderate right skewed distribution, while the kurtosis values were 0 for *Cassiope tetragona*, -1.42 for *Cerastium arcticum* and -0.95 for *Pedicularis hirsuta* indicating the distribution is not leptokurtic (leptokurtic = kurtosis > 3) (Balanda and MacGillivray, 1988). There were significantly higher flower counts of species at more southern Iqaluit than species at more northern Lake Hazen ($t = 4.67$, $P < 0.0001$, $N = 318$ (Lake Hazen), 553 (Iqaluit)).

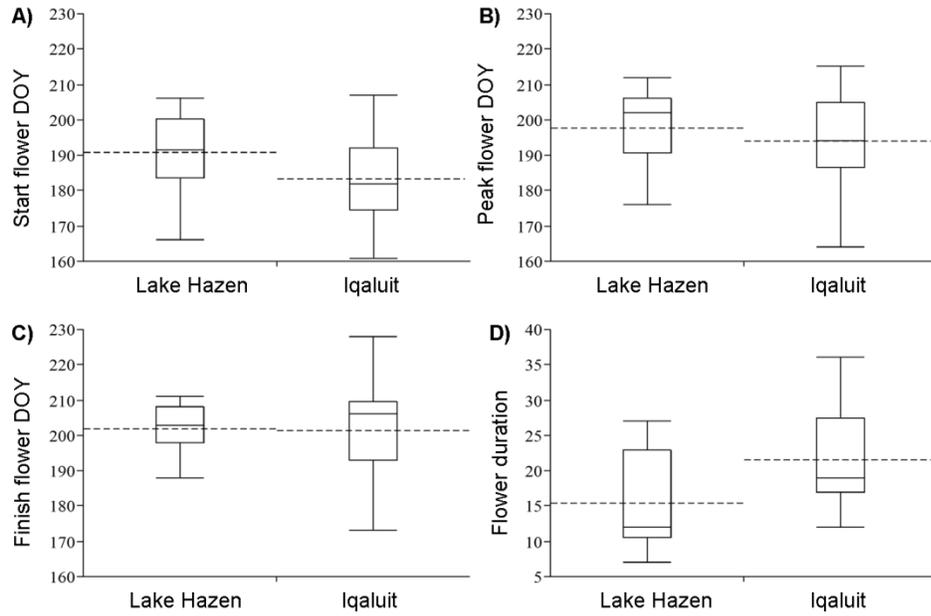


Figure 2.2. Comparison of mean start, peak, finish and duration of flowering across species at Lake Hazen, Ellesmere Island, Nunavut versus Iqaluit, Baffin Island, Nunavut in 2013: A) flowering started significantly earlier at Iqaluit than at Lake Hazen ($t = 2.02$, $P = 0.039$, $N = 22$, 8 days earlier 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 ($t = 2.06$, $P = 0.918$, $N = 13$) and D) flowering duration was significantly longer at Iqaluit than at Lake Hazen ($t = 2.06$, $P = 0.038$, $N = 13$, 6 days longer at Iqaluit). The box plots show the quartiles and mean (dotted line) flowering day of year (DOY) and flowering duration. Reprinted with permission from The University of Chicago Press.

Table 2.2. 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 negative value indicates that the Lake Hazen species flowered earlier or for a shorter duration ($P < 0.0001$, ** $P < 0.001$, * $P < 0.05$). Reprinted with permission from The University of Chicago Press.**

Species (family)	Mean flowering difference (Hazen - Iqaluit)			
	Start	Peak	Finish	Duration
<i>Alopecurus magellanicus</i> (Poaceae)	-2.78 ***	-2.78 ***	-4.43 ***	-4.43 *
<i>Arctagrostis latifolia</i> (Poaceae)	-8.03 ***	-8.03 ***	-9.05 ***	-9.05
<i>Arnica angustifolia</i> (Asteraceae)	2.62 *	0.38	-2.61 *	-2.61 ***
<i>Bistorta vivipara</i> (Polygonaceae)	-1.11	-5.12 **	-	-
<i>Cardamine bellidifolia</i> (Brassicaceae)	-5.53 *	-8.24 *	-10.93 *	-10.93
<i>Cassiope tetragona</i> (Ericaceae)	4.64 **	5.58 ***	4.14 **	4.14
<i>Cerastium arcticum</i> (Caryophyllaceae)	-5.81 ***	-6.31 **	-3.87 *	-3.87
<i>Chamerion latifolium</i> (Onagraceae)	-11.54 ***	-18.00 ***	-25.83 ***	-25.83 ***
<i>Dryas integrifolia</i> (Rosaceae)	-5.95 ***	-10.87 ***	-17.14 ***	-17.14 ***
<i>Eriophorum scheuchzeri</i> (Cyperaceae)	4.00 ***	2.50 ***	-11.97 ***	-11.97 ***
<i>Eutrema edwardsii</i> (Brassicaceae)	8.86 ***	7.93 ***	5.87 ***	5.87 ***
<i>Pedicularis hirsuta</i> (Orobanchaceae)	-3.51 *	-4.53 **	-10.26 ***	-10.26 ***
<i>Saxifraga cespitosa</i> (Saxifragaceae)	-0.61	2.48	-	-
<i>Saxifraga oppositifolia</i> (Saxifragaceae)	3.70 *	4.87 **	5.86 ***	5.86 *
<i>Saxifraga tricuspidata</i> (Saxifragaceae)	-3.55 **	-6.26 ***	-	-
<i>Silene acaulis</i> (Caryophyllaceae)	-2.40 *	-5.59 ***	-2.29	-2.29
<i>Silene uralensis</i> (Caryophyllaceae)	-13.67 ***	-12.74 ***	-11.10 ***	-11.10
All species	-3.73 ***	-4.60 ***	-9.58 ***	-8.75 ***

Table 2.3. Linear mixed effects model results with species as a random effect showing most of the variation in the 2014 start, peak, finish, or duration of flowering of tagged plants was explained by sub-locale and very little was explained by elevation and location (Lake Hazen, Ellesmere Island, Nunavut versus Iqaluit, Baffin Island, Nunavut) where N is the number of tagged plants. Reprinted with permission from The University of Chicago Press.

	Overall model			Location			Elevation			Sub-locale [Location]		
	R^2	P	N	F	DF	P	F	DF	P	F	DF	P
Start flowering	0.77	<0.0001	1380	4.10	1	0.0432	3.51	1	0.0613	32.85	6	<0.0001
Peak flowering	0.78	<0.0001	1380	0.55	1	0.4578	0.05	1	0.827	26.38	6	<0.0001
Finish flowering	0.78	<0.0001	1116	12.85	1	0.0004	7.52	1	0.0062	15.95	6	<0.0001
Flower duration	0.39	<0.0001	1116	0.11	1	0.7349	0.23	1	0.630	4.75	6	<0.0001

Table 2.4. 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 where N is the number of tagged plants. Reprinted with permission from The University of Chicago Press.

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

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: $R^2 = 0.70$, $\rho = 0.84$, $P < 0.0001$, $N = 17$) (Figure 2.3 and Figure A1.1) 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 in 2014 were also consistent between Lake Hazen and Iqaluit (start of

flowering: $R^2 = 0.80$, $\rho = 0.85$, $P < 0.0001$, $N = 17$; finish of flowering: $R^2 = 0.52$, $\rho = 0.71$, $P < 0.005$, $N = 14$) (Figure A1.2) 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 ($R^2 = 0.20$, $\rho = 0.35$, $P > 0.1$, $N = 13$).

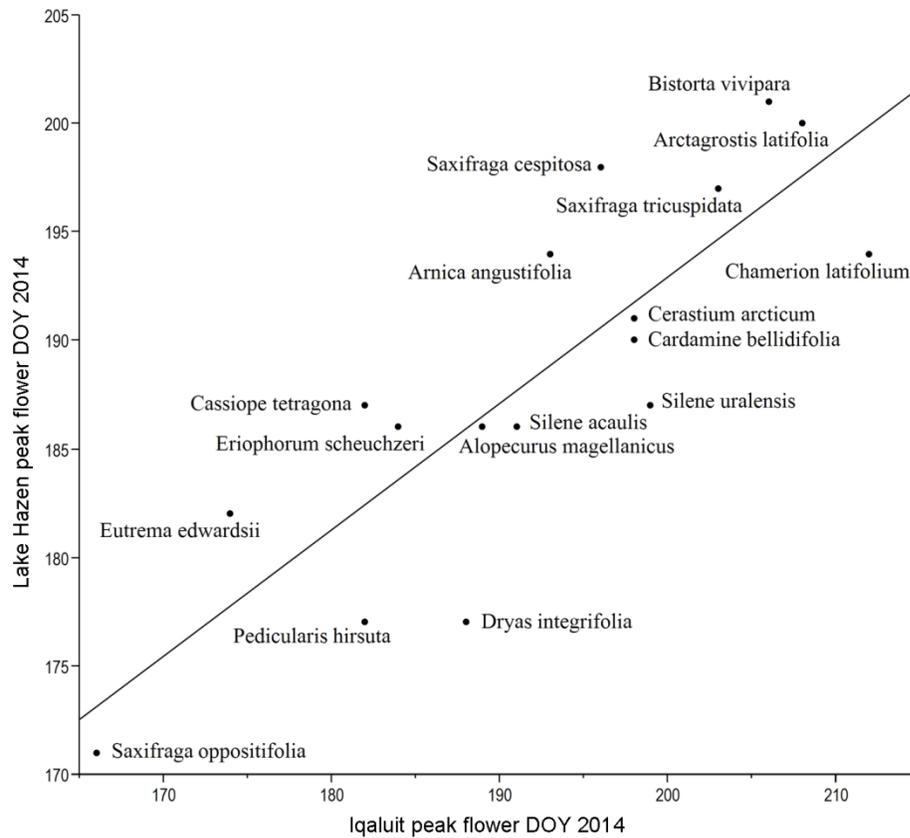


Figure 2.3. Comparison of order of peak flowering day of year (DOY) by species in 2014 at Lake Hazen, Ellesmere Island, Nunavut and Iqaluit, Baffin Island, Nunavut showing that the order of peak flowering is consistent between Iqaluit and Lake Hazen ($R^2 = 0.70$, $\rho = 0.84$, $P < 0.0001$, $N = 17$).

Reprinted with permission from The University of Chicago Press.

Mean temperature at 5 cm above ground across sub-locales was 11.1 °C at Lake Hazen and 11.3 °C at Iqaluit (18th June – 28th July 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 2.5). Average temperatures at 5 cm above ground differed amongst sub-locales at Iqaluit and at Lake Hazen (Table 2.5). At Lake Hazen the mid-elevation sub-locale (451 m.a.s.l.) was, as expected, warmer than the high-elevation sub-locale (781 m.a.s.l.) but also warmer than sub-locales at lower elevations (161 and 287 m.a.s.l.) because of the cooling effect of the frozen lake on low-elevation sub-locales close to the lake. Similarly, at Iqaluit, Sylvia Grinnell Park (50 m.a.s.l.) sub-locale was colder than the other two sub-locales (33 and 105 m.a.s.l.) because of its proximity to a frozen river and the ice-covered ocean.

Table 2.5. Mean daily maximum, minimum and mean temperatures 5 cm above ground (°C) (18th June - 27th July 2014) at sub-locales at Lake Hazen, Ellesmere Island, Nunavut and Iqaluit, Baffin Island, Nunavut. Reprinted with permission from The University of Chicago Press.

Lake Hazen sub-locale	Elevation	Mean	Max	Min
Camp Hazen	161 m	11.3	16.2	6.6
Skeleton Lake	287 m	11.2	16.5	4.6
McGill Mtn plateau	451 m	12.6	19.9	5.3
McGill Mtn upper slopes	784 m	9.4	14.3	5.5
Iqaluit sub-locale				
Apex	33 m	11.7	22.7	4.2
Sylvia Grinnell	50 m	10.5	21.1	2.5
Road to Nowhere	105 m	11.6	19.0	7.5

2.5 Discussion

With dramatic climate change occurring in the Arctic, my 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 my northern location, Lake Hazen, tend to flower earlier and for a shorter period of time than conspecific plants at my southern location, Iqaluit. I had expected the opposite, given that

temperatures are warmer at Iqaluit than at Lake Hazen with a greater number of growing degree days (Table 2.1) and higher daily maximums at Iqaluit (Table 2.5) and 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 at Iqaluit. However, in 2013, a particularly cold, short growing season, plants at Lake Hazen, although they started flowering later than 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 further 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 out of 23 species).

Our findings concur with common garden experiments and long-term studies showing earlier and shorter duration of flowering of plants from further north, where the authors hypothesise the phenological difference in conspecifics is potentially due to evolutionary adaption 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). My approach, however, was different in that the conspecific plants I studied were left growing *in situ* while the common garden experiments moved the conspecific plants/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 further study and, in my study, comparison of only two latitudes was also a limiting factor. Snow melt-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 snow melt-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., 2013b; Bjorkman et al., 2015) but other Arctic studies, particularly where snow accumulation is low, did not find a relationship between time of flowering and snow melt-out date (Thórhallsdóttir, 1998; Molau et al., 2005; Ellebjerg et al., 2008; Bienau et al., 2015). Although mean annual snowfall (1981-2010) at Iqaluit is greater than at Eureka, the number of days in June with snow accumulation is only 1.4 days different (Table 2.1) and hence it seems unlikely that the difference in flowering times between Lake Hazen and Iqaluit is due to differences in snow melt-out date. Photoperiod could also be a contributing factor to earlier flowering at Lake Hazen than at Iqaluit. However, both locations experience 24 hours of day-light per day at least one month before the earliest plants start to flower and hence photoperiod also seems unlikely to be a contributing factor to the difference in flowering time.

While 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 days, 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/day or approximately 2.5 days later per degree of latitude, which suggests that there should be a much greater difference in

phenology across latitudes than I 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 than winter months (Przybylak, 2003). My own temperature data showed only a small difference in temperatures between Lake Hazen and Iqaluit and the difference in the June-August 30-year mean between Iqaluit and Eureka was 2.2°C. Because 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 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. While it is often assumed that temperatures are colder at higher elevations, this is not the case at Lake Hazen and Iqaluit where proximity to frozen water bodies can also influence the temperature and hence why elevation may not have been a strong contributing factor to flowering time in my study. Phenological records, such as herbarium specimens, that 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 localised 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 sub-locales at a location (Lake Hazen versus Iqaluit) than between those two distant locations, possibly suggesting phenotypic plasticity of plants between sub-locales and evolutionary adaptation at different distant locations (Roy et al., 2015). My temperature measurements at plant height support this finding in that there was greater variation in temperature between sub-locales at a location than between locations. The combination of Arctic plant phenological responses to varying climates suggest 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 towards 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 in order to maximise reproductive success. The presence of open flowers for a longer period after peak flowering than before peak flowering, i.e. a right skewed distribution of open flowers, may confer an evolutionary advantage where plants continue to open a small number of flowers opportunistically in the hopes that, if favourable conditions continue, viable seed will be produced (Crimmins et al., 2014). There is only a short finite period before peak flower when conditions are favourable to start flowering because of the constraints of winter conditions and the required prefloration period (Eriksen et al., 1993; Molau, 1997). However, after peak flowering, there can be a longer

period of favourable conditions for flowering when plants develop fruit. The significantly higher flower abundance at Iqaluit than Lake Hazen is also what might be expected given the harsher environment at Lake Hazen and also suggests the potential for greater reproductive success at a southern than 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, my results show that the timing of flowering of Arctic species in the Canadian Arctic Archipelago can be earlier further north and is explained more by sub-locales than latitude or elevation. Given that my 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.

In this chapter I compared the flowering times of Arctic conspecifics using field observations collected by myself and my field assistants at Lake Hazen and Iqaluit. While monitoring the phenology at Lake Hazen, I observed vast differences in flower abundance over three years (2013-2015) which could have implications for reproductive success of Arctic plants as the climate warms. The next chapter documents the flower abundance differences and the implications.

3 Chapter: Arctic plants produce vastly different numbers of flowers in three contrasting years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada

3.1 Abstract

To maximise reproductive success in the short Arctic growing season, plants pre-form flower buds one or more years prior to flowering. Flower bud production depends on warm ambient temperatures. Thus, although currently Arctic plants have low rates of sexual reproductive success, the warming climate may increase reproductive success. Following the long, warm growing season in 2012, plants at Lake Hazen, Ellesmere Island, produced many flowers in the short, cold growing season of 2013. Conversely, few flowers were produced in 2014, a long, warm growing season, but many flowers were produced in 2015, another long, warm growing season. Potentially higher rates of reproductive success in a warming climate could be compromised if consecutive years do not have long, warm growing seasons.

This chapter is reprinted with permission from Ottawa Field-Naturalists' Club:
PANCHEN, Z.A. 2016. Arctic plants produce vastly different numbers of flowers in three contrasting years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. *Canadian Field-Naturalist* 130: 56–63.

3.2 Introduction

To maximise sexual reproductive success in the short Arctic growing season and to minimise time spent developing flower buds at the beginning of the growing season, many Arctic plants pre-form their flower buds in the year or years prior to flowering (Sørensen, 1941). Of the complete flora of 184 species and varieties found in

northeastern Greenland, for example, 80% pre-form their flower buds (Sørensen, 1941). Given the circumpolar nature of Arctic flora, a similar proportion of the 125 species known to grow in the vicinity of Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada, likely also pre-form their flower buds (Sørensen, 1941; Porsild and Cody, 1980; Soper and Powell, 1985; Elven, 2003).

The extent to which the pre-formed flower bud primordia differentiate before the onset of winter varies among species but by August, differentiation has reached the extent to which it will differentiate in that year (Sørensen, 1941). By winter, the flower buds of *Cassiope tetragona* (L.) D. Don (Arctic white heather; Itsutit (Aiken et al., 2011); Ericaceae) are fully formed with developed pollen visible, whereas those of *Arnica angustifolia* Vahl (narrow-leaved arnica; Qursuqtainnarmik nunaralik (Mallory and Aiken, 2012); Asteraceae) and some *Pedicularis* L. (Orobanchaceae) species are only partially formed, with anthers and petals visible and the ovary partially formed but no ovules visible (Sørensen, 1941).

Flower abundance of some Arctic and alpine species is influenced by temperatures in the summer or autumn of the preceding year or by snow depth in the winter just prior to flowering. Flower abundance of *Dryas integrifolia* Vahl (mountain avens; Malikkaat (Aiken et al., 2011); Rosaceae) and *Saxifraga oppositifolia* L. (purple saxifrage; Aupilattunnguat (Aiken et al., 2011); Saxifragaceae) at Tanquary Fiord, Quttinirpaaq National Park, Ellesmere Island, Nunavut, is influenced by August and October mean minimum temperature, respectively, in the year preceding flowering (Panchen and Gorelick, 2015). In Zackenbergdale, Greenland, the flower abundance of *Cassiope tetragona*, *Salix arctica* Pall. (Arctic willow; Supitit (Aiken et al., 2011); Salicaceae) and

Papaver radicum Rottb. (Arctic poppy; Igutsat niqingit (Mallory and Aiken, 2012); Papaveraceae) are influenced by the sum of temperatures above 0°C (heat sum) in the preceding year's growing season, while flower abundance of *Dryas* species is influenced by snow depth in the preceding winter and heat sum in the preceding and current growing seasons (Høye et al., 2007a; Ellebjerg et al., 2008). In Svalbard, Norway, *Cassiope tetragona* flower abundance is influenced by snow depth in the context of extreme weather events, where shallow snow depth and an extremely warm spell in mid-winter resulted in reduced flower numbers the following summer (Semenchuk et al., 2013). In the alpine setting of the Rocky Mountains in Colorado, flower abundance of *Delphinium nelsonii* Greene (Twolobe Larkspur; Ranunculaceae) was influenced by snow depth in the preceding winter, where it is thought that shallower snow depths in more recent years may have exposed the flower buds to frost damage (Inouye and McGuire, 1991). In the same area, flower abundance of *Androsace septentrionalis* L. (pygmyflower rockjasmine; Primulaceae), an annual or short-lived perennial, was influenced by the preceding year's summer precipitation and May temperature in the year of flowering but not the preceding year's growing season temperatures (Inouye et al., 2003).

The Canadian Arctic Archipelago experienced dramatically different weather during each of the growing seasons from 2012 to 2015, leading to growing season lengths and temperatures that differed substantially over the four years. At Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut (81.82°N, 71.35°W), 2012 and 2015 were warm years with long growing seasons, while 2013 was a cold, snowy year with a short growing season and 2014 was a dry year with very little snow and a growing season length and temperatures intermediate between 2013 and 2015. Vastly more flowers were

observed on plant species at Lake Hazen in 2013 and 2015 compared with 2014. This article presents critical baseline natural history data on Canadian High Arctic flowering phenology in a part of Canada that is rarely surveyed. Moreover, it documents the effects of variable weather conditions on Arctic plant flower production.

3.3 Materials and methods

The flowering progression of three species, *Arnica angustifolia*, *Cassiope tetragona* and *Pedicularis capitata* Adams (capitate lousewort; Kukiujait (Aiken et al., 2011); Orobanchaceae), was monitored at Lake Hazen, Quttinirpaaq National Park, from 13th June to 31st July in 2013, 2014 and 2015 (Figure 3.1). A population of the perennial *Arnica angustifolia* was monitored on a southwest facing stream bank southeast of McGill Mountain (81.85°N, 71.35°W), a population of the woody species *Cassiope tetragona* was monitored in a northeast facing gully on McGill Mountain (81.95°N, 71.49°W) and a population of the perennial *Pedicularis capitata* was monitored on the shores of Skeleton Lake (81.83°N, 71.48°W). Areas with established populations of each species were selected as monitoring sites before flowering began in 2013, except in the case of *Arnica angustifolia*, which only grows in a few locations at Lake Hazen and was not found until it was already in flower in 2013.

The sites were visited every 3-4 days in all 3 years. In 2013, monitoring was qualitative and subjective, following an approach successfully used by Panchen *et al.* (2012), wherein the date of first flower, peak flowering and finish of flowering of each population were recorded. After reviewing the 2013 results, the approach for subsequent years was changed to counting flowers to provide a more definitive date for start, peak and finish of flowering. Thus, in 2014 and 2015, monitoring was quantitative wherein 30

plants in each population were randomly tagged before flowering started and the number of flowers on each tagged plant was counted every 3-4 days. The inflorescence (capitulum holding many small flowers) of *Arnica angustifolia* was counted as a single flower.

The start, peak and finish of flowering date for each species were determined from the flower count of the tagged plants. Start of flowering was defined as the date on which open flowers (Figure 3.1) were first observed on the 30 tagged plants, peak flowering as the date on which the greatest number of open flowers was counted and finish of flowering as the first date at the end of flowering on which no open flowers were observed. For each species, the peak number of flowers produced on the 30 tagged plants and the number of tagged plants that flowered in 2013–2015 were compared. For 2013, the peak number of flowers produced on 30 plants and the number of plants flowering out of 30 plants were estimated from observational field notes and photographs of the population or individual plants when they were in peak flower.

May to September mean monthly temperatures for the individual years 2012-2015 and the 10-year (2001–2010) and 30-year (1981–2010) means at Eureka Weather Station, Ellesmere Island, Nunavut, Canada, were obtained or calculated from Environment Canada (2016) data. The Eureka Weather Station (79.59°N, 85.56°W) is the closest weather station to Lake Hazen and experiences a similar climate, with temperatures between the two locations well correlated (Soper and Powell, 1985; Edlund and Alt, 1989; Thompson, 1994).



Figure 3.1. Flower progression of (A) *Arnica angustifolia* (narrow-leaved arnica) (B) *Cassiope tetragona* (Arctic white heather) and (C) *Pedicularis capitata* (capitate lousewort) at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada, showing flower(s) in bud (Ai, Bi and ii, and Ci), open flowers (Aii and iii, Biii and iv, and Cii and iii) and finish of flowering (Aiv and v, Bv and Civ). Photos: Zoe A. Panchen (panels A and C), Carly Cassey (panel B). Reprinted with permission from Ottawa Field-Naturalists' Club.

3.4 Results

Flower abundance of *Arnica angustifolia*, *Cassiope tetragona* and *Pedicularis capitata* populations was much greater in 2013 and 2015 than in 2014 (Table 3.1, Figure 3.2 and Figure 3.3). Compared with 2014, in 2013 and 2015 there were 1.5 times more flowers on tagged *Arnica angustifolia* plants and 1.5 times more *Arnica angustifolia* tagged plants flowering; 273 times more *Cassiope tetragona* flowers and 2.5 times more *Cassiope tetragona* plants flowering; and 6.3 times more *Pedicularis capitata* flowers and 2.3 times more *Pedicularis capitata* plants flowering (Table 3.1).

Of the four years 2012–2015, 2012 was the warmest growing season with the May–September mean temperature at Eureka 1.81°C and 2.32°C warmer than the 10- and 30-year means, respectively (Table 3.2). The coldest growing season occurred in 2013, with the May–September mean temperature 3.05°C and 2.54°C colder than the 10- and 30-year means, respectively. Mean monthly temperatures were above 0°C for a month longer in 2012, 2014 and 2015 than in 2013 suggesting that 2013 had a shorter growing season than the other 3 years.

Arnica angustifolia and *Pedicularis capitata* started, peaked and finished flowering earlier in 2014 and 2015 than in 2013 (Table 3.3), corroborating temperature data, which indicated that the growing season was likely longer in 2014 and 2015 than in 2013. *Cassiope tetragona* started flowering earlier in 2014 and 2015 than in 2013 and peaked and finished flowering earlier in 2015 than in 2013 and 2014. The *Arnica angustifolia* population was found on the last day at Lake Hazen in 2013 and was deemed to be at or close to peak flowering on that day because no flower buds remained and the majority of the plants had fresh-looking flowers, i.e., few of the ray flowers around the edge of the

capitulum were wilting. Given the time from start to peak flowering at Lake Hazen in 2014 and 2015 of 7 and 4 days, respectively (Table 3.3), *Arnica angustifolia* likely started flowering later in 2013 than in 2014 and 2015.

Table 3.1. Comparison of number of flowers per population on the date of peak flowering (Table 3.3) and number of tagged plants that produced flowers (30 tagged plants in each population) of *Arnica angustifolia* (narrow-leaved arnica), *Cassiope tetragona* (Arctic white heather), and *Pedicularis capitata* (capitate lousewort) over 3 years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. Reprinted with permission from Ottawa Field-Naturalists' Club.

Species	No. flowers on date of peak flowering of 30 tagged plants			No. tagged plants that flowered ($n = 30$)		
	2013*	2014	2015	2013*	2014	2015
<i>Arnica angustifolia</i>	30	20	31	30	20	30
<i>Cassiope tetragona</i>	9000	33	9316	30	12	30
<i>Pedicularis capitata</i>	75	12	76	30	13	30

*2013 numbers are estimates.

Table 3.2. Mean monthly temperature from May to September, 2012–2015, compared with 10-year (2001–2010) and 30-year (1981–2010) means at Eureka Weather Station, Ellesmere Island, Nunavut, Canada (Environment Canada, 2016). Reprinted with permission from Ottawa Field-Naturalists' Club.

Month	2012	2013	2014	2015	10-year mean	30-year mean
May	-9.40	-12.31	-8.50	-12.60	-9.45	-10.20
June	5.40	0.50	1.00	4.30	3.49	3.00
July	8.60	4.45	5.85	9.60	5.50	6.10
August	5.10	-1.14	4.27	4.10	4.19	3.20
September	-2.40	-8.50	-4.62	-5.10	-5.47	-6.40
Average, May–Sept.	1.46	-3.40	-0.40	0.06	-0.35	-0.86
Average, June–Aug.	6.37	1.27	3.71	6.00	4.39	4.10



Figure 3.2. *Arnica angustifolia* (narrow-leaved arnica) population on a southwest facing stream bank, southeast of McGill Mountain, Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. Over 100 flowers are visible in the 2013 photograph (A) and just 20 flowers (marked with white plastic plant tags) in 2014 (B). Both photos are of the same site taken from approximately the same position and angle but B is at a lower magnification than A. The patch of vegetation at the top right of A is on the centre skyline in B and the dip in the centre skyline in A is on the left in B. Photos: Zoe A. Panchen. Reprinted with permission from Ottawa Field-Naturalists' Club.



Figure 3.3. *Cassiope tetragona* (Arctic white heather) in a northeast facing gully on McGill Mountain, Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada with over 300 flowers in 2013 (A) and with just three flowers in 2014 but over 100 flowers/fruits from 2013 still visible (B). Photos: Zoe A. Panchen. Reprinted with permission from Ottawa Field-Naturalists' Club.

Table 3.3. Dates for start, peak, and finish of flowering of *Arnica angustifolia* (narrow-leaved arnica), *Cassiope tetragona* (Arctic white heather) and *Pedicularis capitata* (capitate lousewort) over 3 years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. Reprinted with permission from Ottawa Field-Naturalists' Club.

Species	Year	Start of flowering	Peak flowering (days since start of flowering)	Finish of flowering (days since start of flowering)
<i>Arnica angustifolia</i>	2013	—*	31 July	> 31 July†
	2014	5 July	12 July (7)	22 July (17)
	2015	9 July	13 July (4)	23 July (14)
<i>Cassiope tetragona</i>	2013	12 July	19 July (7)	> 31 July†
	2014	2 July	22 July (10)	> 31 July†
	2015	27 June	8 July (11)	23 July (26)
<i>Pedicularis capitata</i>	2013	18 July	21 July (3)	> 31 July†
	2014	7 July	10 July (3)	13 July (6)
	2015	7 July	10 July (3)	20 July (13)

*Not found until after start of flowering.

†Not finished flowering when the Lake Hazen site was vacated on 31st July.

3.5 Discussion

The number of flowers in populations of three Arctic plant species at Lake Hazen was dramatically different in 2014 than in 2013 and 2015. There were many flowers in a year with a cold, short growing season (2013) following a year with a warm, long growing season (2012). There were few flowers in a year with a warm, long growing season (2014) following a year with a cold, short growing season (2013). There were many flowers in a year with a warm, long growing season (2015) following a year with a warm, long growing season (2014). Possible reasons for the low flower abundance in 2014 could be that the 2013 growing season might have been too short or temperatures may not have been warm enough for the species to pre-form flower buds (Sørensen, 1941; Høye et al., 2007a; Ellebjerg et al., 2008; Panchen and Gorelick, 2015). In 2013,

the mean temperature in August, the month in which flower bud differentiation is suspended (Sørensen, 1941), was already below freezing but was above freezing in 2012, 2014 and 2015. Another possible reason is that the three species may have exhausted their available nutrient and carbohydrate resources in the sexual reproductive cycle in 2013 and, hence, did not have enough resources available to pre-form buds in 2013 for the 2014 flowering season. Arctic plants are generally resource limited and may not flower every year as they must build up enough nutrients and carbohydrates over 1 or more years for the resource-intensive sexual reproductive cycle (Mooney and Billings, 1960; Fox and Stevens, 1991; Wookey et al., 1993; Pielou, 1994).

Of the three species studied, *Cassiope tetragona* is the only one considered a snow bed species, it relies on the insulation of snow cover to protect the above ground pre-formed flower buds from the harsh Arctic winters (Soper and Powell, 1985). At Lake Hazen, it grows in gullies, depressions and on the lee side of hills where snow drifts form. In 2013, the gully on McGill Mountain was filled with approximately 30 cm of snow on 20th June and was not free of snow until 2nd July. In 2015 there was approximately 10 cm of snow in the gully on 13th June and it was snow free by 24th June. In 2014, however, the gully was snow free before 14th June. *Cassiope tetragona* may have had fewer flowers in 2014 than in 2013 and 2015 due to the absence of a protective snow layer and the resulting exposure may have killed the pre-formed flower buds (Inouye, 2008; Semenchuk et al., 2013). *Arnica angustifolia* and *Pedicularis capitata* are perennials and their pre-formed buds are protected below ground from the cold air temperatures that are typically -40°C during the winter (Soper and Powell, 1985; Thompson, 1994).

The strategy to maximise sexual reproductive success by pre-forming flower buds in the prior year or years can only be effective if consecutive years have a long, warm growing season; the first year must be long enough and warm enough to pre-form sufficient flower buds (Høye et al., 2007a; Ellebjerg et al., 2008; Panchen and Gorelick, 2015), the second year must be long enough and warm enough to produce viable seed and a subsequent year must be long enough, warm enough and wet enough to produce surviving seedlings (Müller et al., 2011).

Arctic plants have low rates of sexual reproductive success because temperatures are often too low and the growing season too short to produce viable seed (Callaghan, 2005; Müller et al., 2011; Alsos et al., 2013), hence, reproduction is mostly vegetative. Indeed many Arctic species, particularly late-flowering species, have evolved viviparous and bulbil strategies to compensate for the low sexual reproductive success (Molau, 1993a). In addition, the prostrate growth form and rhizomatous root system of many Arctic plant species facilitates the clonal nature of Arctic plants. In theory, warmer temperatures and longer growing seasons resulting from recent climate change should increase sexual reproductive success (Bliss, 1971; Wookey et al., 1993; Müller et al., 2011; Alsos et al., 2013). However, the extreme events and more varied climate, also associated with recent climate change (Easterling et al., 2000a; b; Semenchuk et al., 2013), might be problematic for sexual reproductive success of Arctic plants given the 2+ year cycle to produce flowers (Inouye and McGuire, 1991; Inouye, 2008; Semenchuk et al., 2013). The observations did not test sexual reproductive success *per se*, however, flower abundance can be used as a proxy for reproductive success. If there are few flowers, then the possibility of sexual reproduction is lower.

The difference in methods between 2013 and 2014–2015 and the lack of quantitative measurements in 2013 introduces some uncertainty into the findings. However, the difference between the years is so dramatic that even if the flowers had been counted rather than estimated in 2013, the same results and conclusions would likely have been drawn.

The 2012–2015 observations at Lake Hazen may be indicative of larger-scale processes that could affect Arctic plant populations. Decreased rates of sexual reproduction resulting from increasingly greater year-to-year variation in growing conditions are likely to have important and long-lasting consequences in Arctic ecosystems (Soper and Powell, 1985; Pielou, 1994; Svoboda and Freedman, 1994).

The findings and observations from this chapter and chapter 2 provide insight into current reproductive phenology at two locations in Nunavut. The next three chapters utilise these insights to investigate the impacts of climate change on the flowering and fruiting times of Nunavut Arctic plants. Specifically, the findings and observations from chapters 2 and 3 were utilised to make decisions on what species to study in chapter 4, 5 and 6 and assist in interpreting the findings. These next three chapters employ different spatial and temporal scales and three different methodological approaches to investigate the phenological climate change impacts.

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

4.1 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. One 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 mid-summer. 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. I found no relationship between flowering time and snowmelt date. My findings suggest that Arctic community level ecological effects from climate change induced phenology changes will differ from those in temperate regions.

This chapter is reprinted with permission from Canadian Science Publishing:
PANCHEN, Z.A. and 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 Science* 1: 45–58. DOI 10.1139 /AS-2015-0016.

4.2 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 time responses to climate change in temperate regions are less well studied than flowering time responses 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, 2012b). 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, I 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., 2007b).

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 (Elven, 2003; Aiken et al., 2011). 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 mid-summer. 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, my hypothesis is that later-season flowering plants are flowering earlier and Arctic plant fruits in general are maturing earlier, which I test herein with the *S. oppositifolia* and *D. integrifolia* Tanquary Fiord, Quttinirpaaq National Park data set. I 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. I also address which Tanquary Fiord monthly temperatures are rising.

4.3 Materials and methods

4.3.1 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 (Figure 4.1A).

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 (Figure 4.1) (Raillard, 1999).



Figure 4.1. 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. Reprinted with permission from Canadian Science Publishing.

4.3.2 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. *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 (Figure 4.2A). A *D. integrifolia* fruit was considered to have twisted fruit when its styles had extended and twisted around each other (Figure 4.2B). 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, I summed the number of flowers and summed the number of fruits per visit per year. I determined peak flower and peak fruit day of year for each year for both species. I 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 (Figure 4.2A), causing flowers to continue to be counted beyond the true open flower stage.



Figure 4.2. (A) Mature fruit stage of *Saxifraga oppositifolia* and (B) twisted fruit stage of *Dryas integrifolia*. Reprinted with permission from Canadian Science Publishing.

4.3.3 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. I 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, I 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, I reconstructed the Tanquary Fiord monthly temperatures from the Eureka, Ellesmere Island, Nunavut, Environment Canada Weather Station temperature data (Environment Canada, 2016) using the method described by Leathers et al. (2008) and Panchen et al. (2012) (Table A2.1). 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). I 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.

4.3.4 Statistical analysis

To account for inter-annual variation, I 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, I 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. I 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. I 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 4.1). To determine if time of flowering of each species is related to the snowmelt date, I ran a regression with peak flower day of year as the response variable and first snow-free date as the independent variable. I 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, I ran regressions of Tanquary Fiord annual and monthly mean minimum, mean maximum, and mean temperatures versus year. I also assessed the 1989–2014 average monthly temperature variation through the year. I used the JMP11 software package (SAS Institute, Cary, North Carolina, USA) for all statistical analyses.

4.4 Results

4.4.1 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: $R^2 = 0.46$, $P = 0.003$, $N = 17$) (Figure 4.3). 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 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: $R^2 = 0.03$, $P = 0.4769$, $N = 17$) (Figure 4.3). 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 4.1). *Dryas integrifolia* flowering time advanced 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 4.1). *Dryas integrifolia* fruiting time advanced 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 4.1). *Saxifraga oppositifolia* flowering time advanced 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 4.1). There was no relationship between peak flower day of year and snowmelt date for either species ($N = 18$, *S. oppositifolia*: $R^2 = 0.12$, $P = 0.1638$, and *D. integrifolia*: $R^2 = 0.01$, $P = 0.6813$).

Much of the variation in the peak number of *D. integrifolia* flowers was 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 ($R^2 = 0.13$, $P = 0.7072$, $N = 20$).

Table 4.1. 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. Reprinted with permission from Canadian Science Publishing.

	Overall model			Year β (P)	April temperature β (P)	May temperature β (P)	June temperature β (P)	July temperature β (P)
	R^2	P	N					
<i>Dryas integrifolia</i>								
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)
<i>Saxifraga oppositifolia</i>								
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)

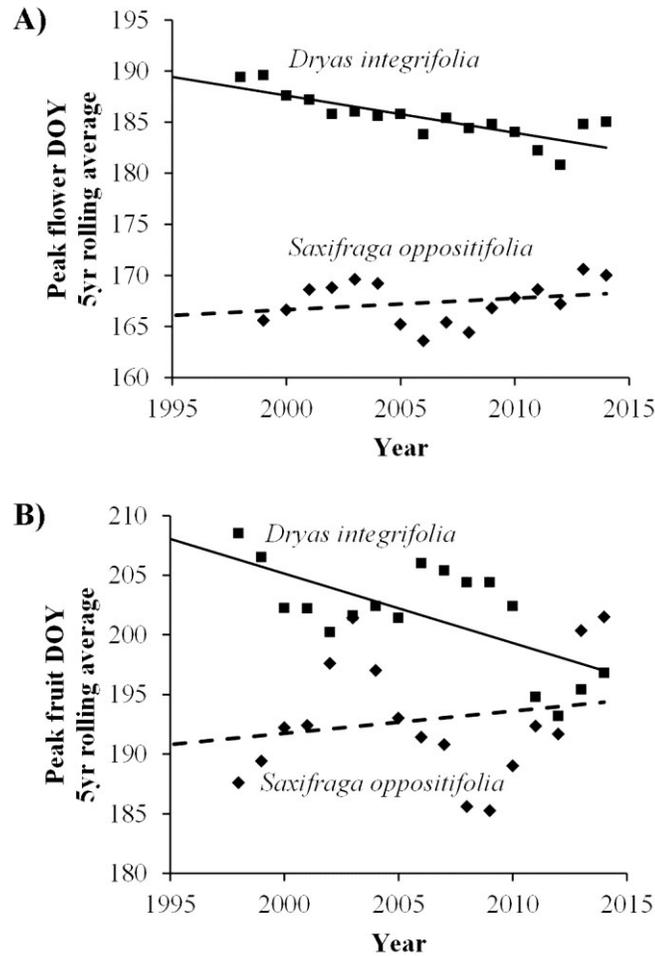


Figure 4.3. (A) Peak flower and (B) peak fruit day of year (DOY) 5-year rolling average from 1994 to 2014 at Tanquary Fiord, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada, showing that *Dryas integrifolia* (squares and solid trend line) had a significant trend towards earlier flowering 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 ($R^2 = 0.03$, $P = 0.4769$, $N = 17$). Reprinted with permission from Canadian Science Publishing.

4.4.2 Temperature

The annual mean minimum, mean maximum, and mean temperatures at Tanquary Fiord have risen significantly over the past 25 years (Figure 4.4A; Table 4.2). There is a

significant trend towards warmer temperatures for January, March, July, August, September, and October (either at $\alpha = 0.05$ or $\alpha = 0.10$) (Figure 4.4B; Table 4.2). The annual and monthly mean minimum temperatures are rising more than the annual and monthly mean maximum and mean temperatures (Figure 4.4; Table 4.2).

The Tanquary Fiord average 1989–2014 monthly temperature varied little across the months of January, February, and March, hovering at approximately $-35\text{ }^{\circ}\text{C}$ (Figure 4.5; Table A2.2). Temperatures rose dramatically in April and May to above $0\text{ }^{\circ}\text{C}$ by the start of June. Temperatures in June, July, and August varied between months by approximately $5\text{ }^{\circ}\text{C}$. Temperatures dropped dramatically in September and October and less steeply in November and December.

Table 4.2. Tanquary Fiord change in annual and monthly mean maximum, mean, and mean minimum temperatures from 1989 to 2014 (β = slope in $^{\circ}\text{C}/\text{year}$, dark grey = significant at $\alpha = 0.05$, and pale grey = significant at $\alpha = 0.10$). Reprinted with permission from Canadian Science Publishing.

	Monthly mean maximum temperature ($^{\circ}\text{C}$)			Monthly mean temperature ($^{\circ}\text{C}$)			Monthly mean minimum temperature ($^{\circ}\text{C}$)		
	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	0.0269	0.02	0.540	0.062	0.04	0.320	0.0926
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	0.4889	-0.0633	0.00	0.7465	-0.030
May	0.00	0.930	-0.006	0.00	0.7927	0.016	0.01	0.6767	0.0266
June	0.00	0.9008	0.0069	0.01	0.6971	0.021	0.02	0.483	0.0346
July	0.13	0.0757	0.0932	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	0.1633	0.0612	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	0.0683	0.05	0.2714	0.095	0.09	0.154	0.0118
December	0.04	0.3238	0.1286	0.06	0.2567	0.139	0.08	0.1663	0.1589
Annual	0.27	0.008	0.086	0.41	<0.001	0.120	0.47	<0.001	0.142

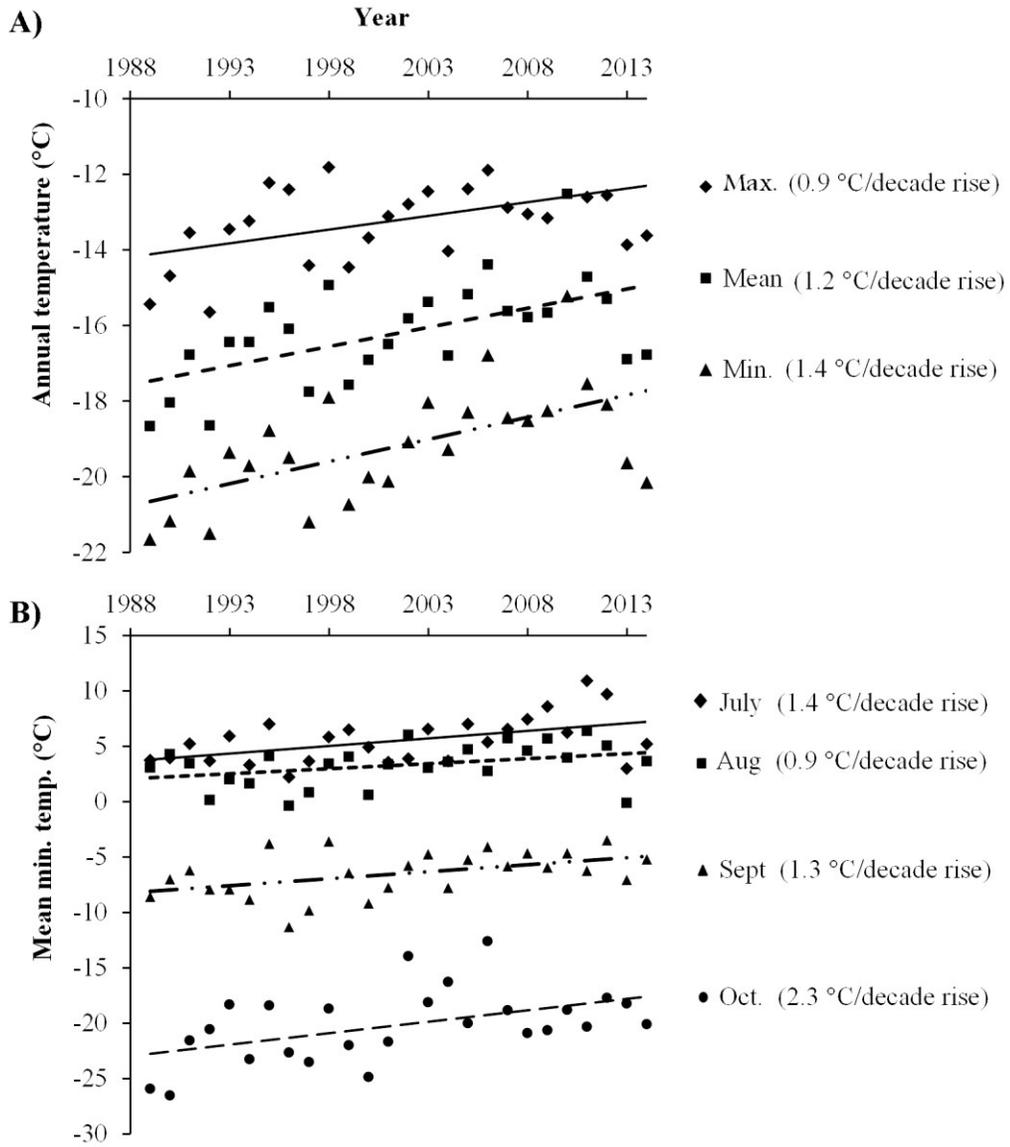


Figure 4.4. Change in temperatures from 1989 to 2014 at Tanquary Fiord, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. (A) Annual mean minimum, annual mean maximum, and annual mean temperatures and (B) July, August, September, and October mean minimum temperatures (Table 4.2). Reprinted with permission from Canadian Science Publishing.

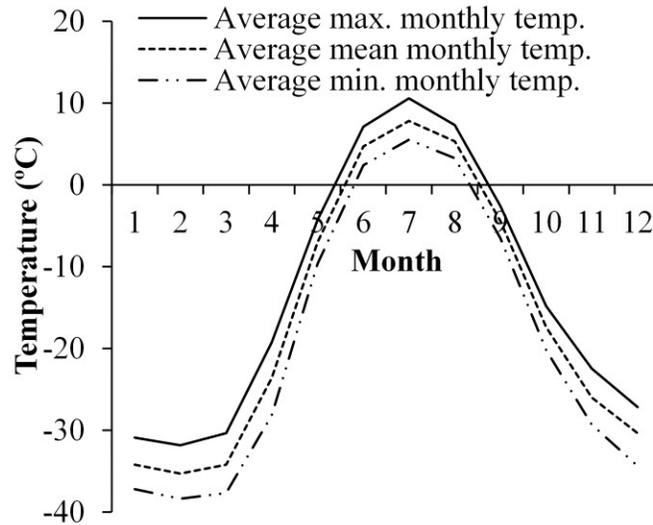


Figure 4.5. Average (1989–2014) monthly mean minimum, monthly mean maximum, and monthly mean temperatures at Tanquary Fiord, Quttinirpaq National Park, Ellesmere Island, Nunavut, Canada (Table A2.2). Reprinted with permission from Canadian Science Publishing.

4.5 Discussion

Flowering and fruiting times of the mid-summer-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 temperatures towards the end of the growing season are warming the most and flowering times are highly dependent on temperatures in the month or two 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., 2012b).

The advance in flowering time of *D. integrifolia* at Tanquary Fiord of 3.6 days/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., 2007a; AMAP, 2012b) and the greater sensitivity of colder climate plants (Cook et al., 2012a) 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.

My 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.

My 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; Prev y et al., 2014). My 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 (Th rhallsd ttir, 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; Stenstr m et al., 1997; Welker et al., 1997; Molau, 2001; H ye et al., 2007a; Cadieux et al., 2008; Ellebjerg et al., 2008).

In addition, Keller and K rner (2003) found *S. oppositifolia* time of flowering not to be sensitive to either temperature or photoperiod, which also supports my findings of no trend towards earlier flowering time for *S. oppositifolia*. However, my 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 under-prediction 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 (Figure 4.4B). 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 inter-annual 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 increases are predominantly occurring at the end of the growing season (and winter) and fruiting times are temperature dependent, I 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., 2007a; Anderson et al., 2012), but in agreement with others (e.g., Kudo and Hirao, 2006; Kimball et al., 2014), I 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 Tanqaury 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 pre-form 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 above ground, while *D. integrifolia* flower buds are below ground. There is likely little snow in October at Tanquary Fiord to insulate and protect the above-ground buds of *S. oppositifolia* when the temperatures drop dramatically (Figure 4.5).

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, 2012b). 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).

My study indicates a different pattern in the response of Arctic plants to a warming climate compared to temperate regions, with the mid-summer-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).

In this chapter I studied the impact of climate change on flowering and fruiting phenology of two Arctic species on a small spatial and temporal scale. The next chapter, chapter 5, investigated the impact of climate change on flowering and fruiting phenology of 23 Arctic plant species, including the two species studied in this chapter, chapter 4, but on a much larger spatial and temporal scale.

5 Chapter: Prediction of Arctic plant phenological sensitivity to climate change from historical records

5.1 Abstract

The pace of climate change in the Arctic is dramatic, with temperatures rising at a rate double the global average. The timing of flowering and fruiting (phenology) is often temperature dependent and tends to advance as the climate warms. Herbarium specimens, photographs and field observations can provide historical phenology records and have been used, on a localised scale, to predict species' phenological sensitivity to climate change. Conducting similar localised studies in the Canadian Arctic, however, poses a challenge where the collection of herbarium specimens, photographs and field observations have been temporally and spatially sporadic. I used flowering and seed dispersal times of 23 Arctic species from herbarium specimens, photographs and field observations collected from across the 2.1 million km² area of Nunavut, Canada to determine (i) which monthly temperatures influence flowering and seed dispersal times, (ii) species' phenological sensitivity to temperature and (iii) whether flowering or seed dispersal times have advanced over the past 120 years. I tested this at different spatial scales and compared sensitivity in different regions of Nunavut. Nunavut's annual temperature has risen 0.2°C/decade since 1946. June temperatures have the strongest influence on flowering time and July temperatures on seed dispersal time. Flowering times have advanced 0.9 days/decade over the past 120 years, while seed dispersal times have advanced 2.1 days/decade, reflecting greater late summer temperature rises in Nunavut. There is great diversity in Arctic plant species' flowering time sensitivity to temperature, with mid-summer-flowering species showing greater sensitivity than early-

or late-flowering species, suggesting climate change implications for Arctic ecological communities, including altered community composition, competition and pollinator interactions. In addition, warming trends and intraspecific temperature-sensitivity varied markedly across Nunavut and could result in greater changes in some parts of Nunavut than in others.

5.2 Introduction

The timing of flowering and fruiting (phenology) is often influenced by temperatures in the month or two preceding flowering or fruiting (Fitter et al., 1995; Panchen et al., 2012; Panchen and Gorelick, 2015). Phenology temperature-sensitivity has been used to identify plants that are indicators of climate change and the responsiveness of plants to climate change (Menzel et al., 2006; Gallagher et al., 2009; Rumpff et al., 2010; Panchen et al., 2012; Springate and Kover, 2014; Bertin, 2015). Herbarium specimens, pressed plants often collected in flower or fruit, provide a reliable historical record of flowering and fruiting phenology for use in phenology-climate change studies (Davis et al., 2015). Many herbarium specimen studies from temperate regions have been used to study flowering time responses to contemporary climate change (Primack et al., 2004; Lavoie and Lachance, 2006; Gallagher et al., 2009; Robbirt et al., 2010; MacGillivray et al., 2010; Neil et al., 2010; Diskin et al., 2012; Panchen et al., 2012; Hart et al., 2014; Davis et al., 2015; Munson and Sher, 2015; Park and Schwartz, 2015). There are, however, few studies on the effects of climate change on the timing of fruiting events (Gallinat et al., 2015) and, to my knowledge, no studies have used herbarium specimens to assess the impacts of climate change on Arctic flowering times or seed dispersal times anywhere in the world. The Arctic is experiencing unprecedented climate change with temperatures

rising at a rate double the global average (Przybylak, 2003; McBean, 2004; Furgal and Prowse, 2007; AMAP, 2012b) and hence the importance of understanding Arctic plant phenological responses to climate change.

In temperate regions, herbarium specimens have often been collected regularly on a local scale enabling the construction of a flowering phenology time series at a single location over extended periods of time and hence most temperate phenology-climate change studies have focused on a localised area with homogeneous topography and climatology. In situations where there are spatial or temporal gaps in the phenology record from herbarium specimens, the phenological historical records have been successfully augmented with dated photographs and field observations (Miller-Rushing et al., 2006; MacGillivray et al., 2010; Robbirt et al., 2010; Panchen et al., 2012; Bertin, 2015). Conducting a similar study in the Arctic, however, poses a challenge (Holopainen et al., 2013). Herbarium specimens, photographs and field observations have only been collected sporadically and, on many occasions, only once from a particular location across the whole of the topographically- and climatologically-varied Nunavut territory, Canada, necessitating a study on large spatial scales. The largest area, to date, used in herbarium specimen climate change phenology analysis is in Ohio, where a 116,000 km² area with 26 weather stations was assessed (Calinger et al., 2013). Nunavut has an area of 2.1 million km² and just 11 weather stations with long-term temperature records. In addition, almost all of the weather stations in Nunavut are coastal and hence influenced by the effect of the sea ice and its melting regime and therefore may not be reflective of temperatures in the interior (Atkinson and Gajewski, 2002).

Long-term studies of flowering and fruiting time temperature-sensitivity of Arctic plants are limited (Thórhallsdóttir, 1998; Cadieux et al., 2008; Ellebjerg et al., 2008; Iler et al., 2013a; Panchen and Gorelick, 2015). However, there have been a number of experimental warming studies on Arctic flowering phenology sensitivity to warming temperatures indicating that many Arctic plants advance flowering in warmer temperatures (Alatalo and Totland, 1997; Jones et al., 1997; Stenström et al., 1997; Welker et al., 1997; Oberbauer et al., 2013; Bjorkman et al., 2015; Khorsand Rosa et al., 2015) but there is evidence that such studies underestimate the phenological impact of a warming climate (Wolkovich et al., 2012). The observed climate change in the Arctic is predominantly in late summer, autumn and winter which may favour advancing seed dispersal phenology over advancing flowering phenology (McBean, 2004; Furgal and Prowse, 2007; AMAP, 2012b; Panchen and Gorelick, 2015).

The primary objectives of this research were to use herbarium specimens, photographs and field observations collected from across Nunavut to determine (i) which monthly temperatures most strongly influence the timing of flowering and timing of seed dispersal of Arctic plants, (ii) the sensitivity of Arctic plant flowering times and seed dispersal times to temperature as an indicator of the impact of climate change on Arctic plant phenology and (iii) whether there has been a change in flowering times and seed dispersal times over the last 120 years in Nunavut. A complementary objective was to assess contemporary climate change with regard to changes in monthly temperatures in Nunavut. More broadly, this research will serve as a proof-of-concept to assess whether phenology-climate change studies using historic data can be conducted at large spatial scales.

5.3 Materials and methods

5.3.1 Flowering time and seed dispersal time data

To determine the flowering and seed dispersal times of 23 common Nunavut Arctic plant species (Table 5.1) over the past 120 years, I examined herbarium specimens collected from across Nunavut, Canada from 1896 to 2015 (Table A3.1). I also included in the dataset flowering and seed dispersal times from field observations at both Lake Hazen, Quttinirpaaq National Park, Ellesmere Island and Iqaluit, Baffin Island, Nunavut in 2013-2015 (Panchen, 2016; Panchen and Gorelick, 2016a) and photographs from the Canadian Museum of Nature's photographic collection and private photographic collections (Table A3.1). I excluded from the dataset herbarium specimens and photographs that were any of the following: south of the tree line, west of longitude 111°W, duplicate herbarium specimens or photographs, or any records of plants not in flower or not dispersing seed. For each herbarium specimen, field observation or photograph (henceforth referred to as a collection data point), I recorded the phenology state (flowering or dispersing seed), collection date representing the time of flowering or time of seed dispersal in number of days from 1st January (henceforth referred to as flowering DOY [day of year] or dispersing seed DOY), year of collection, and latitude and longitude of the collection data point location. The sample size for all collection data points was 3795, with 3353 in flower and 442 dispersing seed. For the field observations, the population's mean peak flowering or peak seed dispersal date at a site was used as the collection date. The 'flowering' phenology state was when the petals were open, i.e. not in a bud, the petals looked fresh and were not wilted or discoloured, and the stigmas and anthers were visible. The 'dispersing seed' phenology state was when the fruit had

dehisced or the styles were extended and untwisted (*Dryas integrifolia* L.) or the capitulum had formed into a spherical seed head (Asteraceae species). There were no dispersing seed collection data points for *Diapensia lapponica* L., *Saxifraga cernua* L. and *Tofieldia pusilla* (Michx.) Pers. In order to compare the phenological sensitivity to temperature in different parts of Nunavut and at different spatial scales, I classified each collection data point by region (Nunavut mainland or Nunavut archipelago), by island (for Nunavut archipelago collection data points only) and by locale (for Lake Hazen or Iqaluit collection data points only) (Figure 5.1 and Figure 5.2). Islands north of Hudson Bay, and Boothia and Melville Peninsulas were classified as Nunavut archipelago. Islands further south and in Hudson Bay were classified with the latitudinally comparable Nunavut mainland.

The 23 species in this study were chosen as follows. First, species with at least 50 herbarium specimens in flower were selected to ensure a large enough sample size. Second, species whose taxonomy was in doubt were eliminated from the analysis. Wind pollinated species were also eliminated because anthesis or receptive stigma are rarely captured or easy to identify on a herbarium specimen. Third, using my phenology monitoring data and observations from Lake Hazen and Iqaluit, species with long flowering durations (> 3 weeks), e.g. *Cassiope tetragona* (L.) D.Don which flowers for 3-4 weeks (Table 3.3, A1.1, A1.2), were eliminated because there would be large variance in flowering DOY. Species where it was difficult to determine whether the plant was in flower e.g. *Qxyria digyna* (L.) Hill were also eliminated from the analysis.

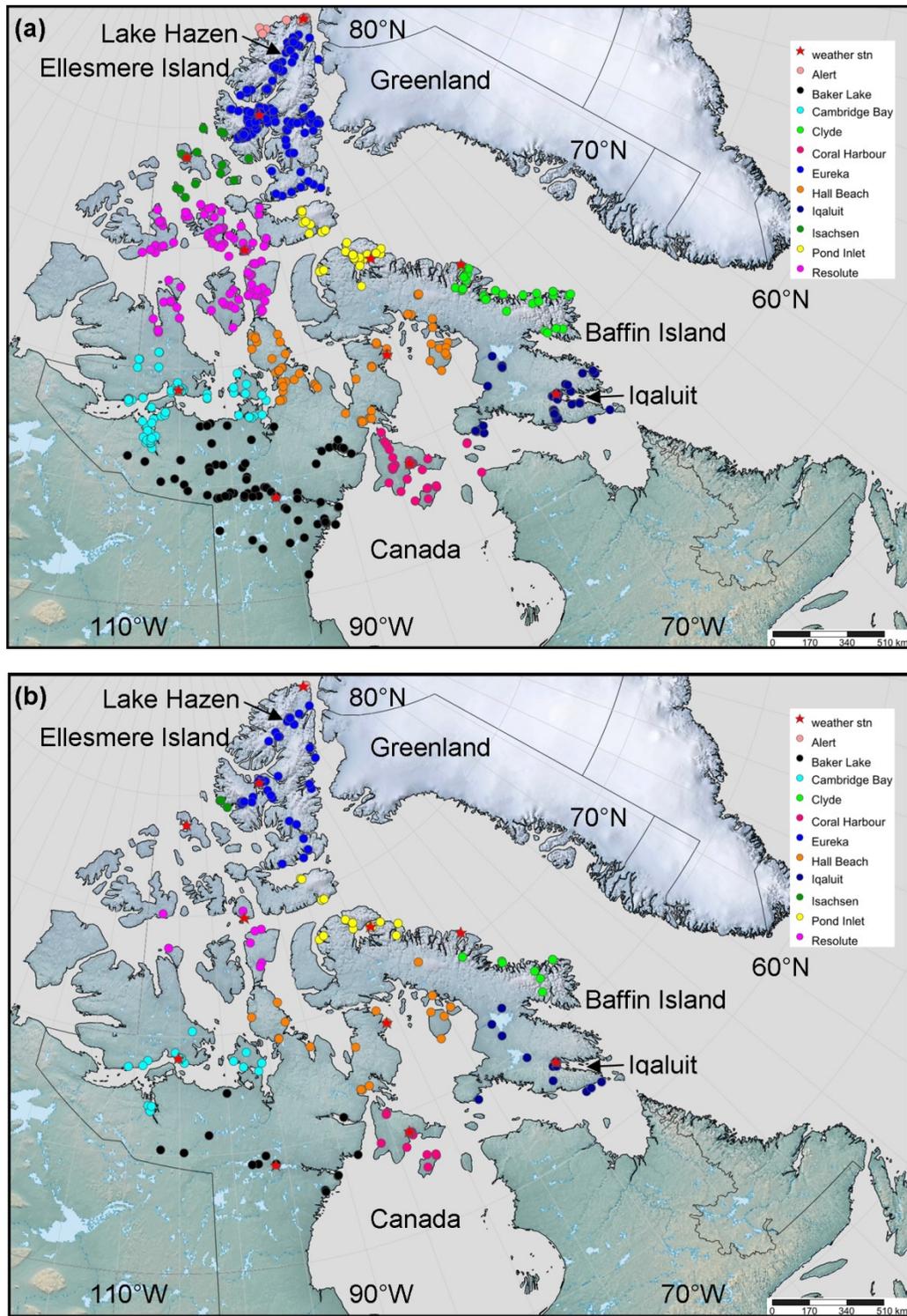


Figure 5.1. Locations of (a) flowering and (b) seed dispersing collections (1946-2015) colour coded by the assigned weather station for each location.

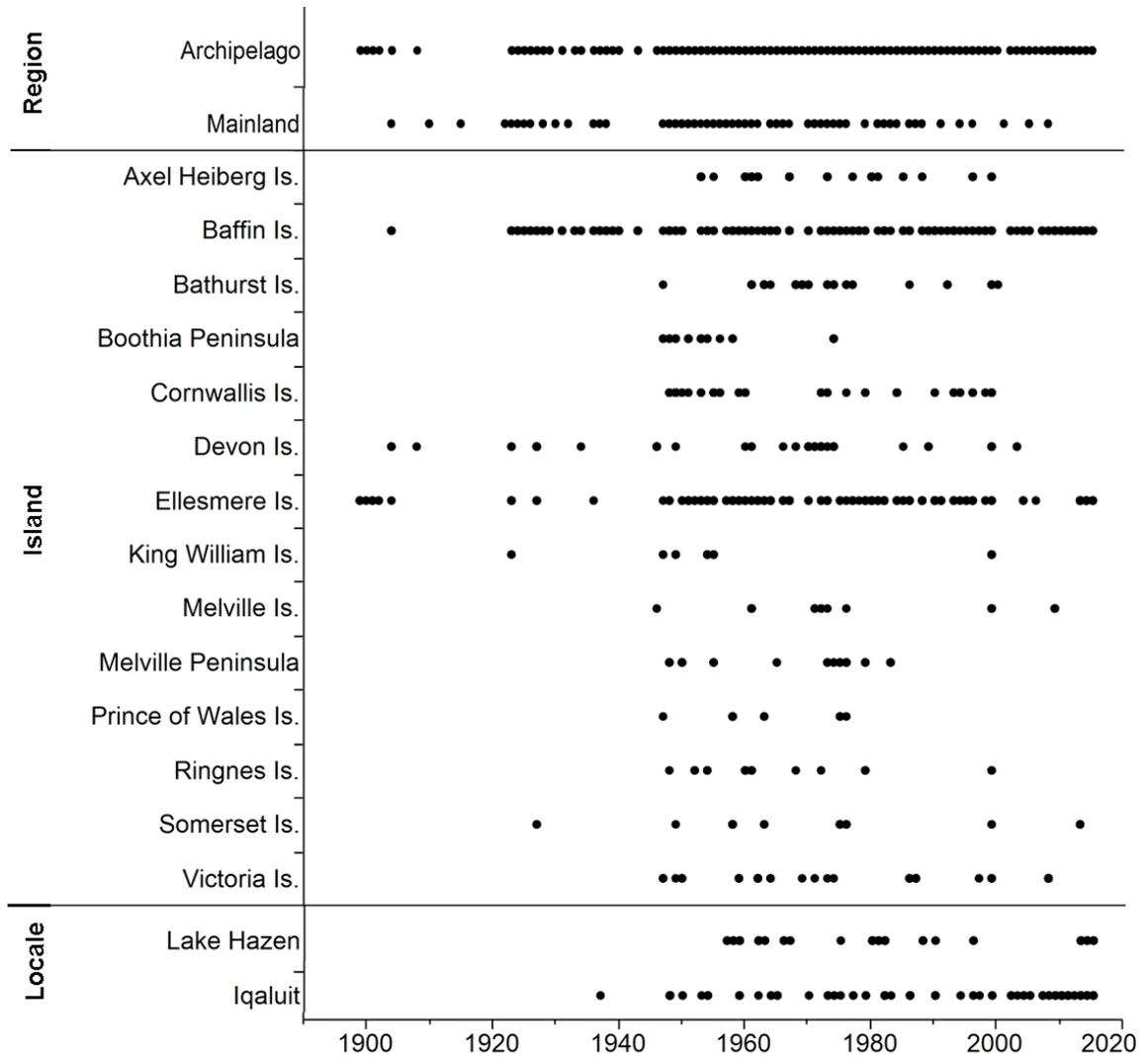


Figure 5.2. Years in which collections were made of flowering and dispersing seed herbarium specimens, photographs and field observations from the Nunavut mainland and Nunavut archipelago regions, Nunavut archipelago islands, and the Lake Hazen and Iqaluit locales. The black markers indicate years in which one or more collections were made.

5.3.2 Temperature data

For the 11 Nunavut weather stations with continuous or close to continuous data from 1946-2015 (Figure 5.1), I extracted monthly mean temperatures directly from Environment Canada's national climate data archive (Environment Canada, 2016) or

calculated monthly mean temperatures from Environment Canada's daily temperature archive data. In some instances the monthly temperatures were missing from the Environment Canada data and, in these cases, I hindcast or reconstructed the monthly mean temperature using data from the closest weather station (Leathers et al., 2008; Throop et al., 2010; Panchen et al., 2012; Panchen and Gorelick, 2015). Each collection data point was associated with the nearest, most climatically logical weather station based on synoptic and sea ice regimes (Fletcher and Young, 1970; Fraser, 1983; Canadian Ice Service, 2002) and hence with that weather station's monthly mean temperatures in the year of collection (Figure 5.1).

5.3.3 Analysis

I calculated the mean flowering time and range of flowering times of each species across Nunavut and classified each species as early-, mid-summer- or late-flowering (Table 5.1). The early-, mid-summer- or late-flowering classification was somewhat subjective wherein species that are traditionally considered early spring-flowerers were classified as early-flowering and the remaining species were divided into equal sized groups with mid-summer-flowerings species' mean flower DOY being mostly earlier than the mean flowering time of all species and late-flowering species' mean flower DOY being mostly later than the mean flowering time of all species. Field observations at Lake Hazen and Iqaluit were also factored into the decision of whether the species would be classified as early-, mid-summer- or late-flowering (Panchen and Gorelick, 2016a). To assess the flowering time differences in early-, mid-summer- and late-flowering species, I compared range of flowering times and the flowering time temperature-sensitivity across Nunavut (described below) of early-, mid-summer- and late-flowering species.

To determine which monthly temperatures most strongly influenced the time of flowering of Arctic plants across Nunavut, I ran a standard least squares mixed model with flowering DOY as the response variable, species as a random effect and May, June, July and August mean temperatures as fixed effects. I repeated this model run separately for each region, each island (Baffin and Ellesmere Islands only) and each locale (Lake Hazen and Iqaluit only), using Nunavut mainland, Nunavut archipelago, Baffin Island, Ellesmere Island, Lake Hazen or Iqaluit flowering collection data points. I ran a similar set of models to determine which monthly temperatures most strongly influence the time of seed dispersal with dispersing seed DOY as the response variable. Baffin Island and Ellesmere Island were chosen from the island classification because they were the only islands with regular collections since 1920 for Baffin Island and since 1957 for Ellesmere Island (Figure 5.2).

To determine the sensitivity of Arctic plant flowering times to temperature, I ran linear regressions for each species from across Nunavut separately with flowering DOY as the response variable and June mean temperature as the explanatory variable. I repeated the regression analyses separately for each region, island and locale in order to compare flower phenology temperature-sensitivity of plants on the Nunavut mainland versus conspecific plants on Nunavut archipelago and similarly Baffin Island plants versus Ellesmere Island conspecifics, and Lake Hazen plants versus Iqaluit conspecifics. There were insufficient data to determine sensitivity of Arctic plant seed dispersal times to temperature per species, hence, I used a standard least squares mixed model to determine the seed dispersal time temperature-sensitivity across Nunavut to July mean temperature across the 20 species with dispersing seed DOY as the response variable,

July mean temperature as the fixed effect and species as a random effect and repeated for Nunavut archipelago, Baffin Island and Ellesmere Island where there were sufficient data.

To determine whether there has been a trend towards earlier flowering times over the past 120 years (1896-2015) across Nunavut, I ran a standard least squares mixed model with flowering DOY as the response variable, species as a random effect and year as a fixed effect. I ran a similar model to determine whether there has been a trend towards earlier seed dispersal times over the past 120 years (1896-2015), with dispersing seed DOY as the response variable.

To assess temperature changes in Nunavut, I correlated monthly mean and annual mean temperatures versus year (1946-2015) for the 11 weather stations. Since there might have been a regime shift over this time period with a cooling period followed by a warming period (Przybylak, 2003; McBean, 2004; Throop et al., 2010; AMAP, 2012a; Reid et al., 2015), I also conducted change point analyses for each of the 11 weather stations for each of annual, June and July mean temperatures separately using a nonlinear least squares model with a prediction formula for the change point of $(B_0 + (B_1 * \text{Year}) + (B_2 * (\text{If Year} \geq C, \text{Then } (\text{Year} - C) \text{ else } 0)))$. All statistical analysis was conducted using JMP12 (SAS Institute, Cary, North Carolina, USA).

5.4 Results

There is considerable variation in flowering DOY of each species over the 120 years (Table 5.1, Figure 5.3a). The species with the least variation was *Erysimum pallasii* (Pursh) Fernald, with a range of 43 days. The species with the greatest variation in flowering DOY was the snow bed species *Ranunculus nivalis* L., with a range of 88 days.

While the sample size is too small statistically, the range of flowering DOY for mid-summer-flowering species is less than for early- and late-flowering species (mean range of 56.9 days versus 65.5 and 67.7 days respectively) (Figure 5.3b). In other words, there is greater variation in the time of flowering of early- and late-flowering species than mid-summer-flowering species, albeit not a statistically significant difference. Similarly, across Nunavut, the flowering time temperature-sensitivity of mid-summer-flowering species was greater than early- and late-flowering species, albeit not statistically significant (mean flowering time temperature-sensitivity of -2.10 versus -1.71 and -1.67 days/°C) (Figure 5.3c). Of the four early-flowering species, the two perennial species, *Ranunculus nivalis* and *Saxifraga oppositifolia* L., have a wide range of flowering times, while the annual/biennial, *Androsace septentrionalis* L., and the short-lived perennial, *Erysimum pallasii*, have a very small range of flowering times. The order of flowering (Figure 5.3a) is consistent with recent observations (Panchen and Gorelick, 2016a), indicating that the collection of flowering time data is representative of species relative time of flowering through the growing season.

Table 5.1. Mean, standard deviation, minimum, maximum and range of flowering day of year (DOY) over the past 120 years (1896-2015) and classification of early-, mid-summer- or late-flowering of 23 plant species as determined from herbarium specimens, photographs and field observations collected from across Nunavut, Canada.

Species	Mean flower DOY	N	Std Dev	Min DOY	Max DOY	Range	Flowering season
<i>Erysimum pallasii</i>	182.6	58	9.1	163	206	43	early
<i>Saxifraga oppositifolia</i>	186.3	282	15.8	145	229	84	early
<i>Androsace septentrionalis</i>	187.3	34	11.4	164	211	47	early
<i>Erigeron compositus</i>	192.2	48	12.9	172	227	55	mid
<i>Ranunculus nivalis</i>	192.6	115	19.0	155	243	88	early
<i>Eutrema edwardsii</i>	194.8	123	12.6	157	227	70	mid
<i>Diapensia lapponica</i>	195.7	57	12.8	173	228	55	mid
<i>Pedicularis hirsuta</i>	195.8	207	12.1	171	233	62	mid
<i>Pedicularis flammea</i>	196.1	71	10.4	177	225	48	mid
<i>Dryas integrifolia</i>	196.4	280	13.8	168	233	65	mid
<i>Ranunculus sulphureus</i>	197.2	155	13.8	166	237	71	mid
<i>Pedicularis arctica</i>	197.7	109	12.9	171	226	55	mid
<i>Pedicularis capitata</i>	199.9	126	11.0	175	226	51	mid
<i>Tofieldia pusilla</i>	202.1	60	8.0	183	220	37	mid
<i>Pedicularis lapponica</i>	202.3	78	12.3	173	237	64	late
<i>Arnica angustifolia</i>	202.7	124	13.6	172	237	65	late
<i>Saxifraga flagellaris</i>	203.8	133	14.5	174	239	65	late
<i>Saxifraga tricuspidata</i>	204.2	227	13.3	172	243	71	late
<i>Saxifraga cespitosa</i>	204.6	340	14.6	164	246	82	late
<i>Chamerion latifolium</i>	205.2	195	10.6	180	237	57	late
<i>Saxifraga cernua</i>	210.0	260	14.0	172	252	80	late
<i>Saxifraga hirculus</i>	210.6	201	15.1	172	245	73	late
<i>Saxifraga aizoides</i>	212.7	70	12.6	188	240	52	late

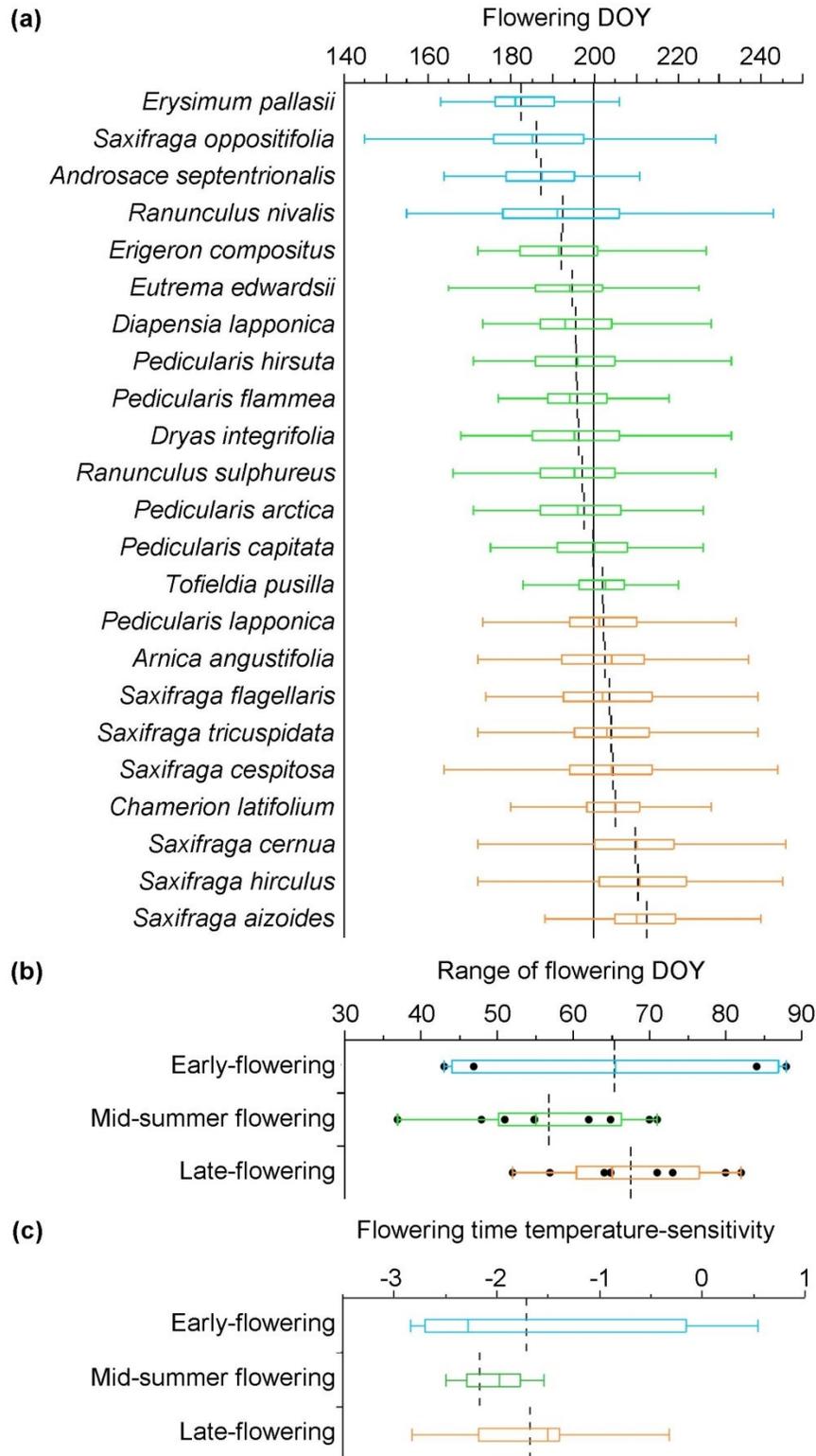


Figure 5.3. (a) Range of flower day of year (DOY) of each species grouped as early- (blue), mid-summer- (green), and late-flowering (orange) species, (b) range of early-, mid-summer-, and late-

flowering species with mean range of flowering DOY (dotted line) of 65.5, 56.9 and 67.7 days respectively and (c) flowering time temperature-sensitivity (β) (days/°C) of early-, mid-summer-, and late-flowering species with mean β (dotted line) of -1.71, -2.10 and -1.67 days/°C respectively.

June mean temperature had the greatest influence on the timing of flowering at all spatial scales, except Ellesmere Island where July mean temperature had the strongest influence (Table 5.2). May to August mean temperatures also had a significant influence on the timing of flowering at some spatial scales. July mean temperature had the greatest influence on the timing of seed dispersal at all spatial scales, except Nunavut mainland where, although not significant, August had the strongest influence (Table 5.3). As expected, in general the AICc values indicate that the models had better fit at finer-grained spatial scales.

Table 5.2. Standard least squares mixed model results at different spatial scales with flowering DOY as the response variable, species as a random effect and May, June, July and August mean temperatures as fixed effects, showing June mean temperature generally has the greatest influence on the time of flowering and models have better fit at finer-grained spatial scales.

	<i>adj R</i> ²	N	AICc	RMSE	May (°C)		June (°C)		July (°C)		August (°C)	
					<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Nunuvut	0.30	3022	23918	12.45	6.97	0.0083	154.47	<.0001	22.56	<.0001	57.75	<.0001
Nunavut mainland	0.23	529	4154	11.74	0.09	0.7642	6.88	0.0090	0.70	0.4027	0.11	0.7443
Nunavut archipelago	0.32	2493	19756	12.48	4.23	0.0399	133.96	<.0001	32.21	<.0001	36.22	<.0001
Baffin Island	0.38	781	6202	12.28	6.82	0.0092	62.93	<.0001	2.15	0.1428	10.68	0.0011
Ellesmere Island	0.29	799	6145	10.91	0.68	0.4090	4.90	0.0272	59.77	<.0001	2.99	0.0840
Iqaluit	0.61	351	2621	9.42	0.08	0.7776	40.37	<.0001	7.00	0.0085	6.04	0.0145
Lake Hazen	0.39	308	2245	8.56	3.15	0.0772	10.44	0.0014	1.28	0.2583	1.42	0.2351

Table 5.3. Standard least squares mixed model results at different spatial scales with dispersing seed DOY as the response variable, species as a random effect and May, June, July and August mean temperatures as fixed effects, showing July mean temperature generally has the greatest influence on the time of seed dispersal and models have better fit at finer-grained spatial scales.

	<i>adj R</i> ²	N	AICc	RMSE	May (°C)		June (°C)		July (°C)		August (°C)	
					<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Nunavut	0.23	346	2694	11.42	0.04	0.8391	0.61	0.4342	41.33	<.0001	21.96	<.0001
Nunavut mainland	0.45	58	449	10.01	0.25	0.6171	0.06	0.8063	0.04	0.8428	2.50	0.1200
Nunavut archipelago	0.26	288	2234	11.29	0.51	0.4760	0.14	0.7099	48.20	<.0001	29.30	<.0001
Baffin Island	0.24	123	953	11.29	0.19	0.6652	1.32	0.2537	14.69	0.0002	0.14	0.7071
Ellesmere Island	0.19	87	646	9.62	6.39	0.0134	0.75	0.3884	15.49	0.0002	9.14	0.0034
Iqaluit	0.63	65	483	8.99	27.35	<.0001	5.30	0.0254	46.96	<.0001	0.09	0.7648
Lake Hazen	-0.29	47	293	5.38	0.06	-	1.20	-	0.69	-	0.03	-

All but two of the 23 species showed a significant negative relationship between time of flowering and June mean temperature, that is, these species flower earlier with warmer June mean temperatures (Figure 5.4, Table A3.2). The magnitude of a species' flowering time sensitivity to June mean temperature varied across Nunavut. The flowering phenology of plants in the Nunavut archipelago was generally more sensitive to June mean temperatures than conspecific plants on the Nunavut mainland and plants on Baffin Island were generally more sensitive than conspecifics on Ellesmere Island. Flowering times at Iqaluit were generally the most sensitive to June mean temperature. Flowering phenology temperature-sensitivity varied dramatically ranging from -1.7 days/°C (*Saxifraga cernua* L. on Nunavut mainland) to -9.6 days/°C (*Diapensia lapponica* at Iqaluit). The annual/biennial, *Androsace septentrionalis*, and the late-flowering *Chamerion latifolium* (L.) Holub were the only species whose flowering time showed no sensitivity to temperature. The seed dispersal time sensitivity to July mean temperature of the 20 species from across Nunavut was -1.79 days/°C (N = 346, P < 0.0001). That is, seed dispersal was 1.79 days earlier for every 1°C rise in July mean temperature. The

seed dispersal time sensitivity to July mean temperature across species was -2.30, -3.65 and -1.64 days/°C in Nunavut archipelago, Baffin Island and Ellesmere Island respectively (N = 288, 123, 87 respectively, $P < 0.0001$).

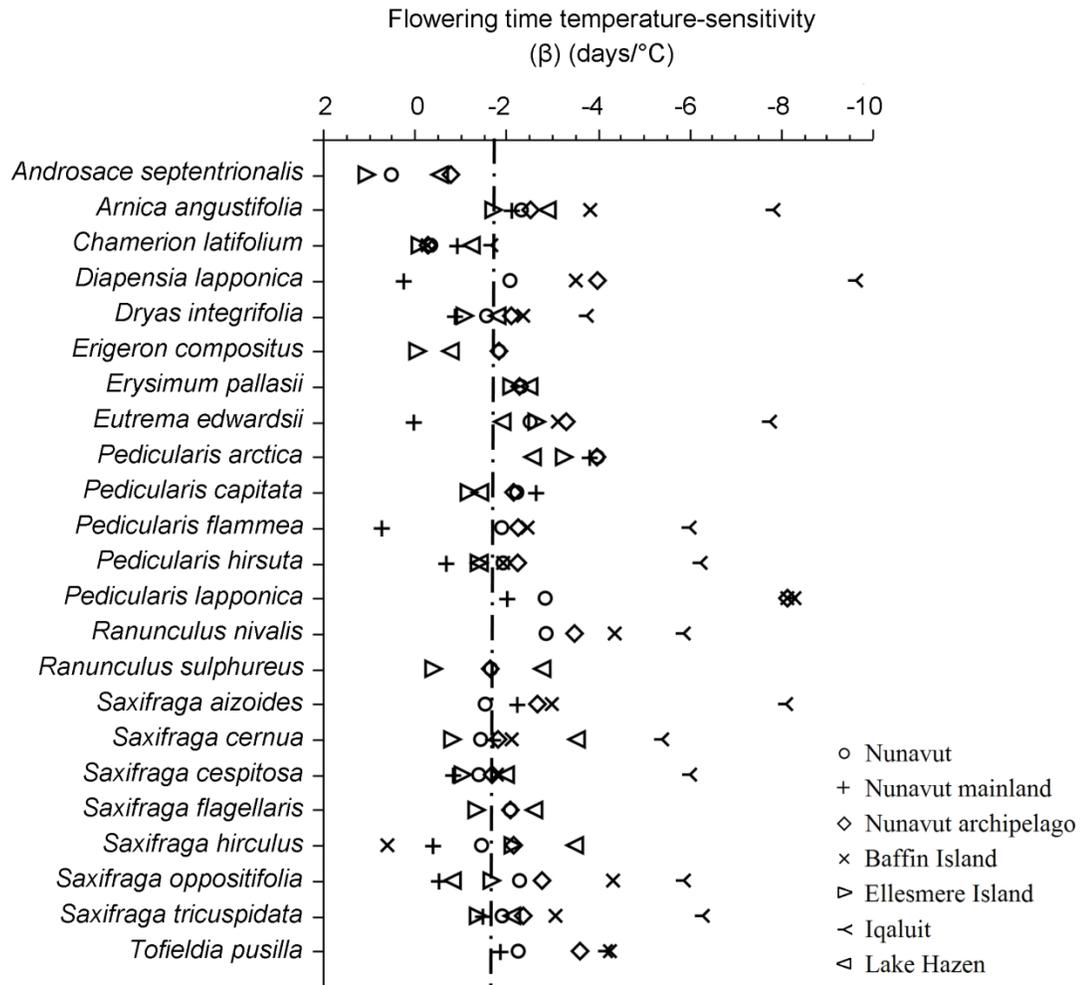


Figure 5.4. Species' flowering time temperature-sensitivity (β) at different spatial scales in Nunavut, Canada. Significant sensitivity is to the right of the dashed vertical line (Table A3.2).

Across Nunavut, plants flowered 0.9 days/decade earlier over the past 120 years (1896-2015) ($R^2 = 0.25$, $N=3353$, $P < 0.0001$) (Figure 5.5a) but dispersed seed 2.1 days/decade earlier over the 120 years ($R^2 = 0.27$, $N=442$, $P < 0.0001$) (Figure 5.5b).

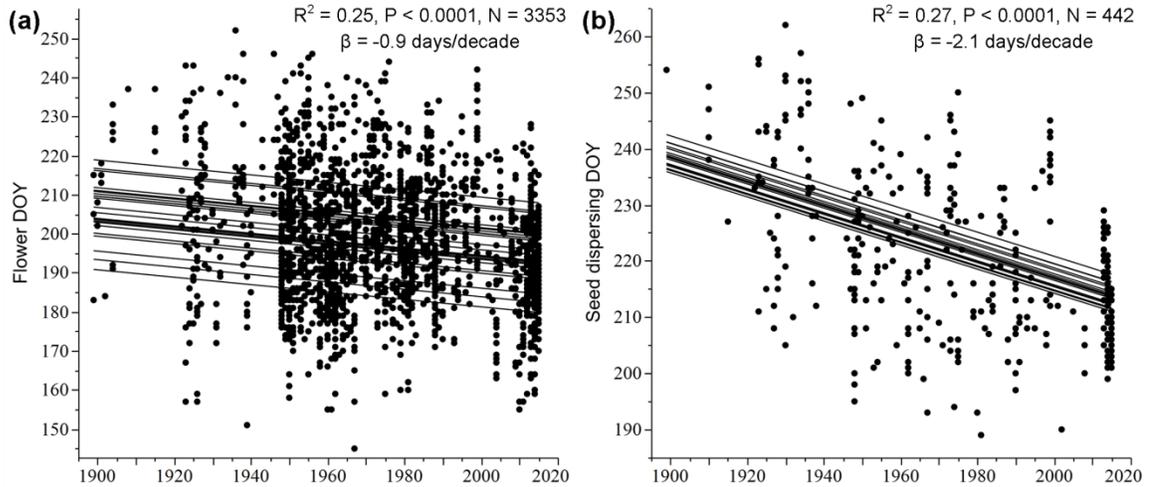


Figure 5.5. Standard least squares mixed model with (a) flowering DOY (Day of Year) and (b) dispersing seed DOY as the response variable, species as a random effect and year as a fixed effect across 23 species (a) and 20 species (b) in Nunavut where β is the days/decade change in flowering or seed dispersal time and trend line represents the best fit for each species.

Annual temperatures have risen significantly since 1946 at nine of the 11 weather stations, albeit with a very weak correlation at Hall Beach (Nunavut archipelago) and Pond Inlet (Baffin Island), while annual temperatures at Clyde (Baffin Island) and Iqaluit (Baffin Island) have not risen significantly (Table 5.4). Baker Lake (Nunavut mainland) and Cambridge Bay (Victoria Island) in the south and west of Nunavut experienced the most dramatic annual temperature increases of 0.30 and 0.35 °C/decade respectively. In contrast, May and August mean temperatures have not risen significantly at any of the 11 weather stations. June mean temperatures have risen significantly since 1946 only at Baker Lake, Cambridge Bay and Pond Inlet and, although significant, very weakly correlated at Coral Harbour (Nunavut mainland) (0.36, 0.33, 0.25 and 0.24 °C/decade respectively). Following a similar pattern to the June mean temperature, July mean temperature has risen significantly since 1946 at Baker Lake, Cambridge Bay, Coral

Harbour, Eureka (Ellesmere Island), Pond Inlet and, although significant, very weakly correlated at Clyde (0.28, 0.30, 0.37, 0.26, 0.37 and 0.17 °C/decade respectively). The most dramatic June mean temperature increases are at Baker Lake and Cambridge Bay with 0.36 and 0.33 °C/decade rise respectively, while the most dramatic July mean temperature increases are at Coral Harbour and Pond Inlet, both rising 0.37°C/decade.

Since 1946, a regime shift has been experienced at Alert, Eureka, Isachsen and Resolute (Nunavut archipelago) weather stations, with a cooling or steady temperature period followed by a warming period with change points in the 1970s to 1980s for annual mean temperatures, the late 1960s and early 1970s for June mean temperatures and 1990s to 2000s for July mean temperatures (Figure 5.6, Table A3.3). Baker Lake and Coral Harbour (Nunavut mainland) and Cambridge Bay (Victoria Island) weather stations experienced an annual mean temperature regime shift from steady temperatures to warming temperatures in 1987, 1964 and 1989, respectively, but no significant regime shift for June or July mean monthly temperatures. Clyde, Hall Beach, Iqaluit and Pond Inlet weather stations experienced an annual mean temperature regime shift from cooling or steady temperatures to warming temperatures but only Pond Inlet has seen a June and July mean temperature regime shift from cooling to warming temperatures in 1985 and 1977 respectively. Large inter-annual variation in monthly and annual temperatures of several degrees Celsius was observed for all weather stations (Figure 5.6).

Table 5.4. Correlation of monthly mean or annual mean temperatures (°C) versus year (1946-2015) for the 11 long-term weather stations in Nunavut, Canada where β is the rate of change in monthly temperature in days/yr. Grey shading indicates a significant warming trend (dark grey = $R^2 \geq 0.1$ and pale grey = $R^2 < 0.1$).

Mean temp	Alert			Baker Lake			Cambridge Bay			Clyde			Coral Harbour		
	R ²	P	β												
Ann	0.18	0.0002	0.02	0.24	<.0001	0.03	0.32	<.0001	0.04	0.01	0.4710	0.00	0.11	0.0055	0.02
Jan	0.08	0.0146	0.04	0.15	0.0008	0.07	0.18	<.0001	0.06	0.00	0.5720	-0.01	0.04	0.0937	0.04
Feb	0.03	0.1689	0.03	0.08	0.0178	0.05	0.17	<.0001	0.06	0.02	0.3041	-0.02	0.00	0.6530	0.01
Mar	0.01	0.3344	0.02	0.01	0.3783	0.02	0.04	0.0963	0.03	0.00	0.5628	-0.01	0.01	0.4609	-0.01
Apr	0.03	0.1548	0.02	0.02	0.2198	0.02	0.06	0.0415	0.03	0.00	0.9122	0.00	0.00	0.7402	0.01
May	0.00	0.7568	0.00	0.02	0.2750	0.02	0.01	0.4500	0.01	0.02	0.2798	-0.01	0.00	0.8130	0.00
Jun	0.01	0.4480	0.01	0.12	0.0031	0.04	0.11	0.0059	0.03	0.01	0.4902	0.01	0.07	0.0263	0.02
Jul	0.01	0.5585	0.00	0.13	0.0021	0.03	0.14	0.0012	0.03	0.07	0.0251	0.02	0.22	<.0001	0.04
Aug	0.01	0.5084	0.00	0.03	0.1869	0.01	0.03	0.1530	0.01	0.11	0.0052	0.02	0.04	0.1104	0.01
Sept	0.17	0.0003	0.04	0.06	0.0463	0.02	0.08	0.0164	0.03	0.09	0.0139	0.02	0.07	0.0257	0.02
Oct	0.11	0.0050	0.04	0.07	0.0220	0.04	0.12	0.0029	0.05	0.00	0.7239	0.00	0.13	0.0024	0.05
Nov	0.06	0.0461	0.03	0.03	0.1383	0.02	0.11	0.0047	0.05	0.01	0.3496	0.02	0.03	0.1405	0.03
Dec	0.12	0.0040	0.04	0.05	0.0664	0.04	0.07	0.0288	0.04	0.02	0.2049	0.02	0.02	0.2235	0.03

Mean temp	Eureka			Hall Beach			Iqaluit			Isachsen			Pond Inlet			Resolute		
	R ²	P	β															
Ann	0.17	<.0001	0.02	0.10	0.0086	0.02	0.02	0.2834	0.01	0.21	<.0001	0.03	0.06	0.0351	0.01	0.19	<.0001	0.03
Jan	0.02	0.2466	0.02	0.02	0.2259	0.02	0.01	0.4898	0.02	0.09	0.0100	0.04	0.01	0.3880	-0.02	0.04	0.0803	0.03
Feb	0.01	0.5567	0.01	0.00	0.9527	0.00	0.01	0.4112	-0.02	0.04	0.0862	0.03	0.00	0.6458	-0.01	0.03	0.1646	0.03
Mar	0.01	0.5088	0.01	0.00	0.7664	0.01	0.00	0.6490	-0.01	0.04	0.1058	0.02	0.01	0.5251	0.01	0.03	0.1320	0.03
Apr	0.05	0.0709	0.03	0.03	0.1525	0.02	0.01	0.5520	0.01	0.10	0.0064	0.04	0.01	0.5580	0.01	0.10	0.0069	0.04
May	0.00	0.8689	0.00	0.00	0.6332	0.01	0.00	0.8365	0.00	0.02	0.2124	0.01	0.00	0.9057	0.00	0.00	0.6406	0.01
Jun	0.05	0.0774	0.02	0.01	0.4395	0.01	0.00	0.7389	0.00	0.03	0.1661	0.01	0.16	0.0006	0.02	0.03	0.1291	0.02
Jul	0.16	0.0005	0.03	0.05	0.0661	0.01	0.01	0.3702	0.01	0.03	0.1640	0.01	0.34	<.0001	0.04	0.05	0.0528	0.02
Aug	0.00	0.7580	0.00	0.03	0.1329	0.01	0.02	0.2209	0.01	0.01	0.3690	-0.01	0.09	0.0120	0.02	0.00	0.8851	0.00
Sept	0.10	0.0084	0.04	0.10	0.0062	0.02	0.04	0.0853	0.01	0.14	0.0014	0.03	0.03	0.1429	0.01	0.11	0.0055	0.03
Oct	0.07	0.0277	0.04	0.14	0.0012	0.06	0.09	0.0115	0.04	0.07	0.0232	0.03	0.03	0.1340	0.02	0.14	0.0018	0.05
Nov	0.08	0.0156	0.05	0.08	0.0215	0.05	0.03	0.1653	0.03	0.12	0.0032	0.05	0.01	0.4003	0.02	0.09	0.0104	0.04
Dec	0.06	0.0444	0.04	0.02	0.2949	0.02	0.02	0.3002	0.03	0.06	0.0376	0.03	0.01	0.4038	0.02	0.05	0.0770	0.03

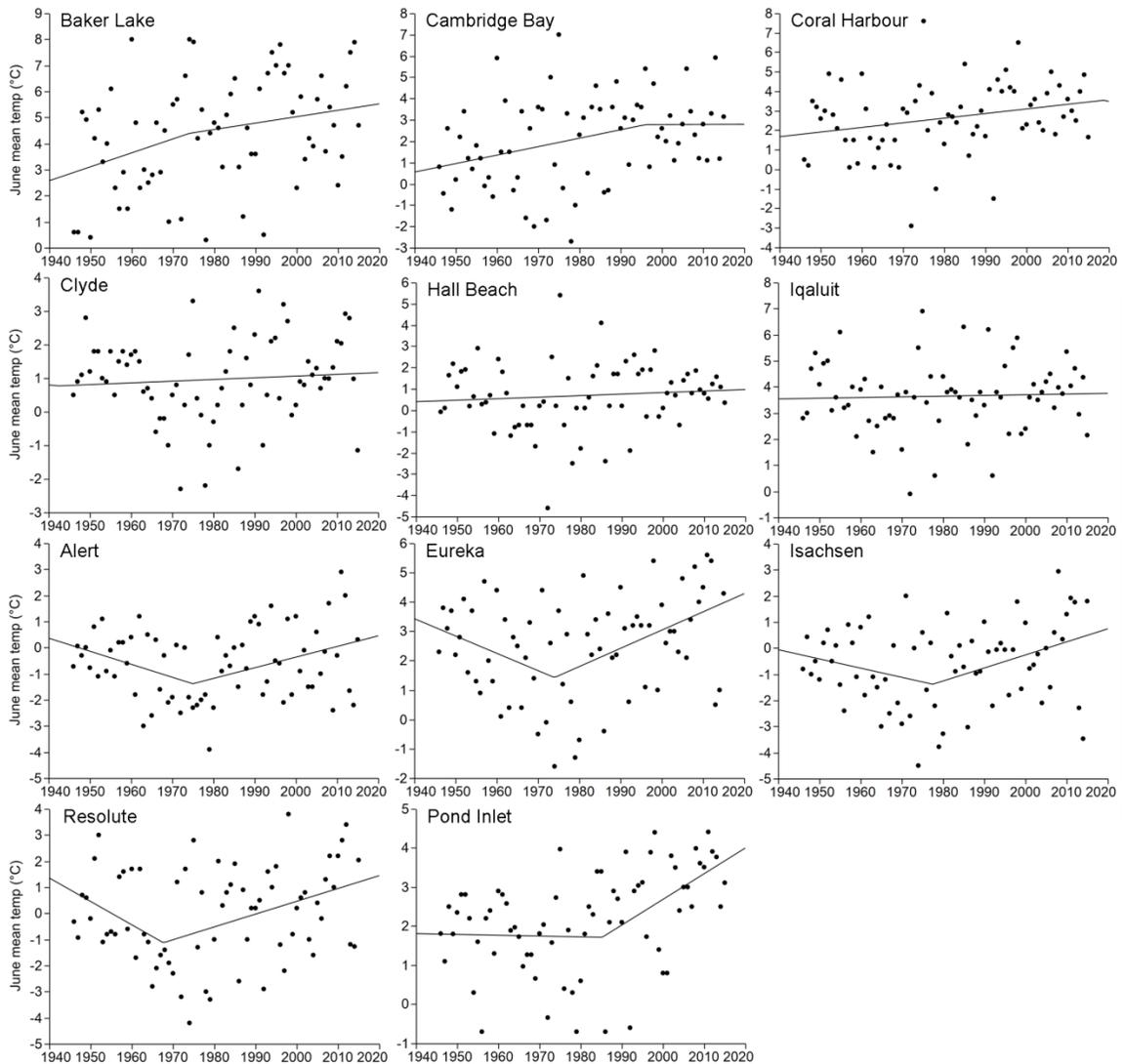


Figure 5.6. June mean temperatures since 1946 with regime shift trend line for the 11 long-term weather stations in Nunavut, Canada (Table A3.2). Baker Lake, Cambridge Bay and Coral Harbour have experienced continually rising temperatures in June since 1946; Alert, Eureka, Isachsen and Resolute have experienced a regime shift from a cooling period to a warming period in June; Clyde, Hall Beach and Iqaluit have experienced no significant warming in June since 1946; and Pond Inlet has experienced a regime shift from a steady temperature to a warming period in June.

5.5 Discussion

Flowering phenology sensitivity to June temperatures varies dramatically among the 23 Nunavut Arctic plant species and in different parts of Nunavut. Different species are known to have different flowering phenology temperature-sensitivity and thus variation among species is to be expected (Ledneva et al., 2004; Miller-Rushing and Primack, 2008; Panchen et al., 2012; Calinger et al., 2013; Mazer et al., 2013; Hart et al., 2014; Kimball et al., 2014). However, the magnitude of the variation and the spatial variation intraspecifically is surprisingly high in contrast to other studies (Wolkovich et al., 2012; Oberbauer et al., 2013) but not unprecedented (Olsson and Ågren, 2002; Wagner and Simons, 2009). Among the spatial scale comparisons, flowering phenology temperature-sensitivity of plants at Iqaluit appears to be the most pronounced but this analysis is on a small spatial scale and hence perhaps temperature-sensitivity is underestimated at the larger spatial scales due to greater variations in the flowering times. Similarly, flowering phenology of plants at Lake Hazen, a small spatial scale, appear to be more temperature sensitive than conspecifics from across Ellesmere Island, a large spatial. Seed dispersal time of the 20 Arctic species also appears to be sensitive to temperature, in contrast to experimental warming studies (Jones et al., 1997; Bjorkman et al., 2015) but in alignment with faster fruit maturation at Zackenberg, Greenland experimental warming sites (Ellebjerger et al., 2008). Only two species, *Androsace septentrionalis* and *Chamerion latifolium*, showed no flowering phenology sensitivity to June temperatures in any part of Nunavut. *Androsace septentrionalis* is an annual, or more often biennial in Nunavut, that must complete its life cycle within the year and whose time of flowering is influenced primarily by snowmelt date (Inouye et al., 2003). *Androsace septentrionalis* also showed

no significant trend to earlier flowering in an alpine community (CaraDonna et al., 2014). The late-summer-flowering *Chamerion latifolium* also showed no sensitivity to July or August mean temperatures (data not shown) suggesting that its flowering time may be triggered by other abiotic factors.

As the Arctic climate warms, the variation in flowering and fruiting phenology sensitivity to temperature among species has implications for Arctic ecological communities, including altered community composition, plant competition and pollinator interactions (Rathcke and Lacey, 1985; Callaghan, 2005; Molau et al., 2005; Ellebjerg et al., 2008; Hegland et al., 2009; McKinney et al., 2012; Høye et al., 2013; CaraDonna et al., 2014; Euskirchen et al., 2014). Mid-summer-flowering species are potentially the species that will show the greatest response to climate change and hence their time of flowering could shift more than early-flowering species resulting in greater overlap of flowering in early- and mid-summer-flowering species and greater pollinator competition. In contrast, there could thus be less overlap in flowering of mid-summer- and late-flowering species possibly resulting in less pollinator competition for late-flowering species and potentially increasing reproductive success of late-flowering species. In addition, variation in warming trends in different parts of Nunavut (Table 5.4 and A3.2 and Figure 5.6) and diverse intraspecific flowering time temperature-sensitivity in different parts of Nunavut suggests that there could be greater changes in some parts of Nunavut than in others. From the warming trend analysis conducted here, the greatest and most immediate changes are likely to be seen in the south and west, i.e. Nunavut mainland and Victoria Island, and the least changes on southern and eastern Baffin

Island. However, this could be counter-balanced by the apparent greater flowering phenology temperature-sensitivity of Baffin Island plants.

Given that a) flowering times and fruiting times are influenced mostly by June and July temperatures respectively and b) compared to June temperatures, July temperatures are warming more and warming across a wider area of Nunavut, it is not surprising that seed dispersal times have advanced over twice as fast as flowering times over the past 120 years in Nunavut. This implies that the seed may be maturing faster because of warmer temperatures and there is potential for greater sexual reproductive success and an extended reproductive season in the short Arctic growing season (Molau, 1993a, 1997; Wookey et al., 1993; Alatalo and Totland, 1997; Klady et al., 2011; Müller et al., 2011). Temperatures in Nunavut are rising predominantly at the end of the growing season and during winter and hence it might be expected that fruiting times may advance more than flowering times (Panchen and Gorelick, 2015). While August temperatures appear not to have risen significantly since 1946, flowering and fruiting times are influenced most by June and July temperatures, respectively. By August, autumn has arrived and leaves are senescing. Hence, the lack of warming trend in August temperatures has little consequence on the assertion that late-season reproductive phenological events are advancing more than early season phenological events.

As expected, the smaller the spatial scale, the better the model fit. However, even at the largest spatial scale, i.e. across the 2.1 million km² of Nunavut, there was a significant relationship between flowering time or seed dispersal time versus monthly mean temperatures. This is surprising given the large geographical area, the large distances between temperature data sources and different year-to-year variations in the synoptic

weather systems across Nunavut (Fletcher and Young, 1970; Fraser, 1983; Furgal and Prowse, 2007). Given the large geographical area included in the analysis, the absolute values of the phenological temperature-sensitivity should be treated with caution; it is the relative values that are important here. The start and end year used in temperature climate change analysis, combined with a greater inter-annual temperature variation than the warming trend, can play a strong role in the magnitude of the warming or phenological trends observed, especially when looking at trends over time (Panchen and Gorelick, 2015; Baker et al., 2016).

Future phenology-climate change studies of Arctic plants might focus on mid-summer-flowering species in order to minimise variance in the analysis, as the range of possible flowering dates appears to be less than for early- or late-flowering species. In addition, flowering-time sensitivity appears to be greater for mid-summer-flowering species, thus responses to climate change may be more readily observed. The two species with the greatest variation in time of flowering, *Saxifraga oppositifolia* and *Ranunculus nivalis*, are either early-flowering and/or snow bed species, groups of species that have been identified by a long-term phenology study in Sweden to be most labile in terms of flowering time (Molau et al., 2005). Arctic species' sequence of flowering is consistent from year-to-year in Nunavut from 1896-2015 and is comparable to the current day (Molau et al., 2005; Panchen and Gorelick, 2016a) (Figure 5.3a). Hence, herbarium specimens can be used to determine species' sequence of flowering.

Temperature changes observed since 1946 can be grouped into three patterns that reflect the three predominant synoptic weather systems in Nunavut. Baker Lake, Cambridge Bay and Coral Harbour are predominantly influenced by continental systems

(Fletcher and Young, 1970; Fraser, 1983) (Figure 5.6) and are experiencing the greatest rises in temperature, both annually and in the months of June and July, and these temperatures have been rising continually since 1946. Alert, Eureka, Isachsen and Resolute are predominantly influenced by Arctic Ocean basin systems (Fletcher and Young, 1970; Fraser, 1983; Edlund and Alt, 1989) and experienced a regime shift from a cooling period to a warming period (Throop et al., 2010; Reid et al., 2015). Clyde, Iqaluit and Hall Beach are influenced by Atlantic Ocean systems and have experienced little or no warming annually or in the months of June and July and no regime shift (Fletcher and Young, 1970; Fraser, 1983; Canadian Ice Service, 2002). Pond Inlet can experience any of the three systems in different years or months and perhaps might explain the regime shift from a steady temperature to a warming period (Fletcher and Young, 1970; Fraser, 1983; Canadian Ice Service, 2002).

In conclusion, June and July mean temperatures have the greatest influence on flowering and seed dispersal times of Nunavut plants respectively. Over the past 120 years, seed dispersal times have advanced twice as fast as flowering times in Nunavut and reflect greater increases in July than June mean temperatures. The diversity in flowering time temperature-sensitivity among species could result in altered community ecology and those changes could vary in different parts of Nunavut given the variation in temperature trends and intraspecific phenological temperature-sensitivity across Nunavut.

In this chapter I studied the impact of climate change on reproductive phenology using historical records. The next chapter employs a different methodology, namely an elevation gradient as a proxy for climate change, to study the impact of climate change on flowering and fruiting phenology of a subset of the species studied in this chapter.

6 Chapter: Space for time: Arctic plant phenological responses to climate change, substituting an elevation gradient as a proxy for the rising temperatures of climate change

6.1 Abstract

Long-term phenological monitoring to study the impacts of climate change is problematic in the Arctic due to the remoteness of the region. An alternative approach to predicting the phenological responses of Arctic plants to climate change is to utilise an elevation gradient, with its associated temperature gradient, as a proxy for climate change. Flowering and seed dispersal times of seven common Arctic plant species were recorded along an elevation gradient by Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. Hourly temperatures at plant height at each site were recorded and the growing degree days required for flowering determined. Six of the seven species showed flowering time sensitivity to temperature but only one of three species studied showed seed dispersal time sensitivity to temperature. *Dryas integrifolia* had the greatest flowering and seed dispersal time sensitivity to temperature, suggesting greater ability to respond to climate change and suggesting that this species has the potential to remain a dominant species in the Arctic landscape as the climate warms. Species required fewer growing degree days to flower at the coldest site compared to warmer sites, suggesting that plants at the coldest site initiate flowering with less heat input. Later-flowering species required more growing degree days to flower than earlier-flowering species. In the short Arctic growing season, late-flowering species are less likely to flower or flower too late to produce seed than early-flowering species. Thus, as

the climate warms, later-flowering species may become more successful at flowering and seed production.

6.2 Introduction

Long-term phenological monitoring to study the impacts of climate change is problematic in the Arctic due to the remote and inaccessible nature of the region. An alternative approach to predicting the phenological responses of Arctic plants to climate change is to substitute space for time by using an elevation gradient, with its associated temperature gradient, as a proxy for the warming effects of contemporary climate change.

For many plant species, the timing of phenological events are affected by temperature (Rathcke and Lacey, 1985). Monthly temperatures leading up to flowering are good predictors of the time of flowering (Fitter et al., 1995; Panchen et al., 2012). In the Canadian Arctic, June mean temperature is the best predictor of the time of flowering and July mean temperature is the best predictor of the time of seed dispersal (Panchen and Gorelick, 2015, 2016b). Flowering is triggered once a cumulative temperature above a threshold is reached, referred to as growing degree days (GDD) (Rathcke and Lacey, 1985; Bernier and Périlleux, 2005; Kimball et al., 2014). The GDD threshold temperature varies from species to species but for Arctic plant species can range from -7°C to $+5^{\circ}\text{C}$ (Ellebjerg et al., 2008; Kimball et al., 2014; Barrett et al., 2015). However, Arctic phenology studies tend to use a threshold of 0°C (Levesque et al., 1997; Molau et al., 2005; Prev y et al., 2014).

While some Arctic studies have utilised an elevation gradient to study differences in phenology, none have employed it to determine phenological sensitivity to temperature (Alatalo and Molau, 1995; Levesque et al., 1997; Lessard-Therrien et al., 2013; Frei et

al., 2014). Some Arctic long-term phenology studies and experimental warming studies have studied flowering phenology sensitivity to temperature but do not report phenological temperature-sensitivity for individual Arctic plant species (Molau, 1997; Stenström et al., 1997; Welker et al., 1997; Larl and Wagner, 2006; Høye et al., 2007a; Khorsand Rosa et al., 2015) but rather compare the relative responses of species grouped by growth form (Arft et al., 1999; Molau et al., 2005; Oberbauer et al., 2013). In addition, sensitivity of fruiting time events to temperature is understudied (Gallinat et al., 2015) with the focus primarily on the effects of temperature on seed viability (Wookey et al., 1993; Alatalo and Molau, 1995; Levesque et al., 1997; Molau, 1997; Stenström et al., 1997; Welker et al., 1997; Arft et al., 1999; Naoya, 1999; Klady et al., 2011). Experimental warming phenological studies may under-estimate the phenological sensitivity of plants to temperature (Wolkovich et al., 2012), suggesting that long-term phenological studies or using an elevational gradient to simulate more natural warming might provide more realistic results.

The objective of this study was to use the elevation gradient by Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada to determine (i) flowering and seed dispersal phenology temperature-sensitivity of seven common Arctic plants species, (ii) GDD requirements for each species and (iii) if species' flowering GDD requirements varied across elevations.

6.3 Materials and methods

6.3.1 Field sites

The field work was conducted at Lake Hazen, a 60 km long lake in Quttinirpaaq National Park on northern Ellesmere Island, Nunavut, Canada (81.8°N, 71.4°W) in June

and July 2015. The Lake is at an elevation of 160 m above sea level (m.a.s.l.) with mountains immediately to the north of the lake rising to approximately 1000 m.a.s.l. I established seven field sites along an elevational gradient between the park warden station on the northern lakeshore of Lake Hazen and the upper slopes of McGill Mountain (1050 m.a.s.l.) immediately north of the warden station. I set up sites where there were established populations of the species of interest. The lowest site was 166 m.a.s.l. and the highest site was 784 m.a.s.l. The top 200 m of McGill Mountain is a steep talus slope with minimal vegetation and hence unsuitable for field sites.

6.3.2 Flowering and seed dispersal data

I randomly tagged thirty plants each of the species *Alopecurus magellanicus* Lam., *Cassiope tetragona* (L.) D.Don, *Dryas integrifolia* Vahl, *Papaver dahlianum* Nordh., *Ranunculus sulphureus* Sol., *Saxifraga oppositifolia* L. and *Saxifraga tricuspidata* Rottb. at three to seven sites along the elevational gradient. Every three to four days, i.e. twice per week, I counted the number of open flowers on each tagged plant and recorded the date on which the largest number of flowers were open on each tagged plant (peak flowering day of year [DOY]). A flower was considered open and counted only when the petals were open and not in a bud, the petals looked fresh and not wilted or discoloured, and the stigma(s) and anthers were visible. I recorded the date on which each plant started to disperse seed (start seed dispersal DOY) for three species (*Dryas integrifolia*, *Papaver dahlianum* and *Saxifraga oppositifolia*). A tagged plant was considered to be starting to disperse seed when at least one fruit had dehisced (*Papaver dahlianum* and *Saxifraga oppositifolia*) or the styles were extended and untwisted (*Dryas integrifolia* L.). *Cassiope tetragona* and *Saxifraga tricuspidata* fruits dehisced after the field season finished and

time of *Alopecurus magellanicus* and *Ranunculus sulphureus* seed dispersal is not obvious, hence these four species could not be included in the seed dispersal study.

6.3.3 Temperature data

I recorded the temperature 5 cm above ground, i.e. at plant height, on an hourly basis at each site using thermistor temperature sensors (TMC6-HD, Onset Computer Corp., Bourne, MA, USA) and data loggers (HOBO H08-006-04, Onset Computer Corp.). June mean temperature and July mean temperature were calculated by averaging hourly temperatures for each month. The daily mean temperature was calculated by averaging the hourly temperature for each day. GDD for each day was calculated as the cumulative sum of daily mean temperatures above 0°C from 1st June 2015 to that day. The daily mean temperature did not rise above 0°C at any site until after 1st June. Sites were then categorised into warmest, coldest and intermediate sites based on GDD.

6.3.4 Analysis

To determine flowering time sensitivity of each species to June mean temperature, I ran a linear regression separately for each species with peak flowering DOY as the response variable and June mean temperature as the explanatory variable. Similarly, I ran linear regressions for seed dispersal time sensitivity to July mean temperature for each species separately with start seed dispersal DOY as the response variable and July mean temperature as the explanatory variable. June mean temperature was used for the flowering time linear regression and July mean temperature for the seed dispersal time linear regression because generalised least squares mixed models (species as random effect, June and July mean temperatures as fixed effects and peak flowering or seed dispersal DOY as the response variable) indicated that June mean temperature was the

most significant explanatory variable for flowering time and July mean temperature was the most significant explanatory variable for seed dispersal time (data not shown) (Panchen and Gorelick, 2016b).

To determine whether there were differences in GDD required to reach peak flowering for each species at the warmest, intermediate and coldest sites, I ran a Tukey-Kramer HSD ANOVA test separately for each species and for all species combined with peak flowering DOY as the response variable and coldest/intermediate/warmest site as the explanatory variable. I also calculated the minimum, maximum and range of GDD for each species, which are presented here as these data might be of interest to those conducting controlled greenhouse experiments. All statistical analysis was conducted using JMP12 (SAS Institute, Cary, North Carolina, USA).

6.4 Results

Six of the seven species flowered significantly earlier with warmer June mean temperatures (Table 6.1, Figure 6.1). *Dryas integrifolia* showed the greatest flowering time sensitivity to June mean temperature by flowering 4.7 days earlier for every 1°C warmer June mean temperature. *Papaver dahlianum* was the only species that showed no significant flowering time sensitivity to June mean temperature. *Dryas integrifolia* dispersed seed significantly earlier with warmer July mean temperatures (4.8 days earlier/1°C warmer) while *Papaver dahlianum* and *Saxifraga oppositifolia* seed dispersal times showed no significant temperature-sensitivity (Table 6.2, Figure 6.2).

Table 6.1. Linear regression of species' peak flowering time day of year (DOY) versus June mean temperature along an elevational gradient, where β is the flowering time temperature-sensitivity (days/°C) with a negative β indicating earlier flowering with warmer June mean temperatures.

Species	R^2	P	N	β
<i>Alopecurus magellanicus</i>	0.24	<.0001	114	-2.756
<i>Cassiope tetragona</i>	0.34	<.0001	149	-3.015
<i>Dryas integrifolia</i>	0.54	<.0001	150	-4.709
<i>Papaver dahlianum</i>	0.00	0.5398	90	-0.137
<i>Ranunculus sulphureus</i>	0.08	0.0072	90	-0.644
<i>Saxifraga oppositifolia</i>	0.18	<.0001	179	-1.602
<i>Saxifraga tricuspidata</i>	0.13	<.0001	120	-1.159

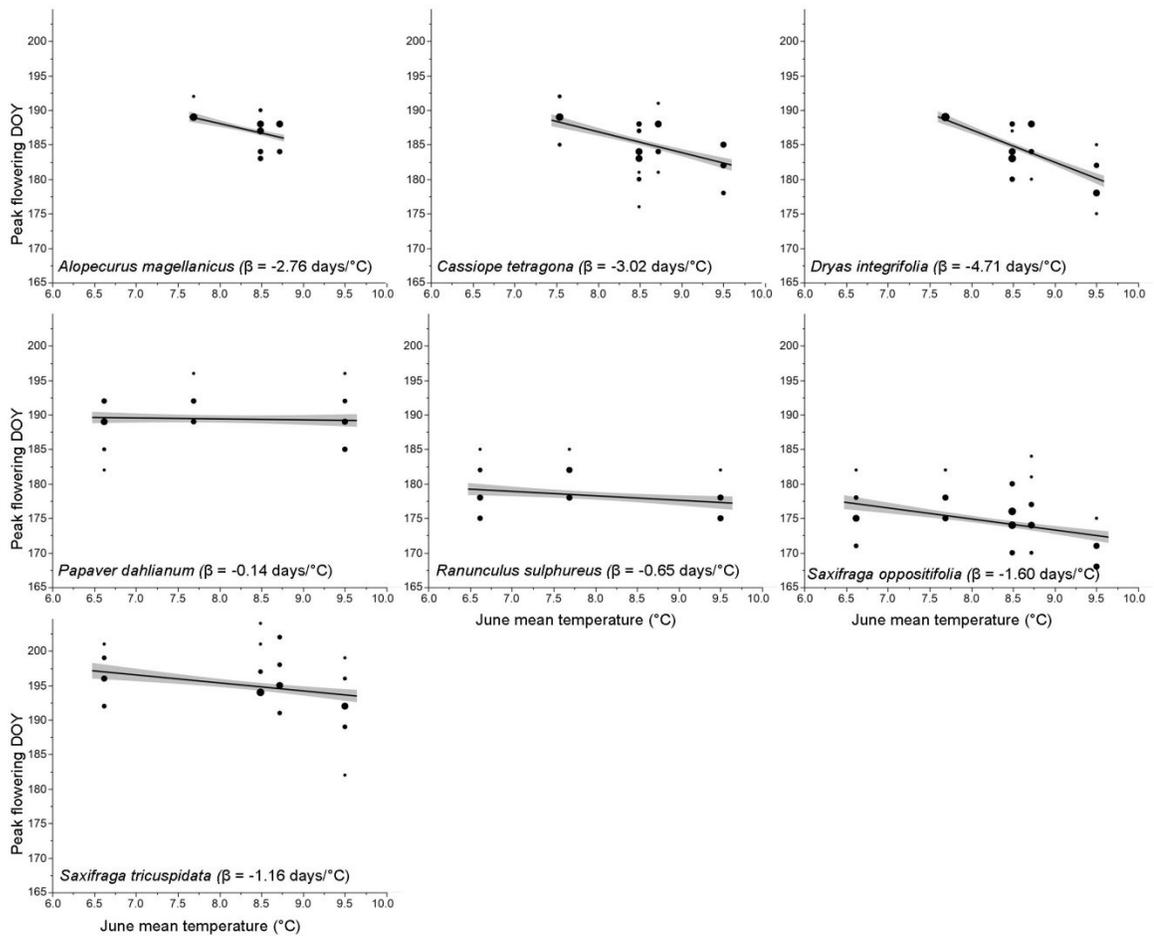


Figure 6.1. Species' peak flowering time (day of year [DOY]) sensitivity to June mean temperature (β) showing how much earlier the species flowers with warmer June mean temperatures (Table 6.1). The size of the points on the graphs is proportional to the number of plants that peak flowered on the DOY and June mean temperature co-ordinate and grey shading indicates the 95% confidence limit.

Table 6.2. Linear regression of species' seed dispersal time day of year (DOY) versus July mean temperature along an elevational gradient, where β is the seed dispersal time temperature-sensitivity (days/°C), a negative β indicates earlier seed dispersal with warmer July mean temperatures.

Species	R^2	P	N	β
<i>Dryas integrifolia</i>	0.30	<.0001	133	-4.799
<i>Papaver dahlianum</i>	0.02	0.1513	90	-0.539
<i>Saxifraga oppositifolia</i>	0.00	0.4927	174	-0.287

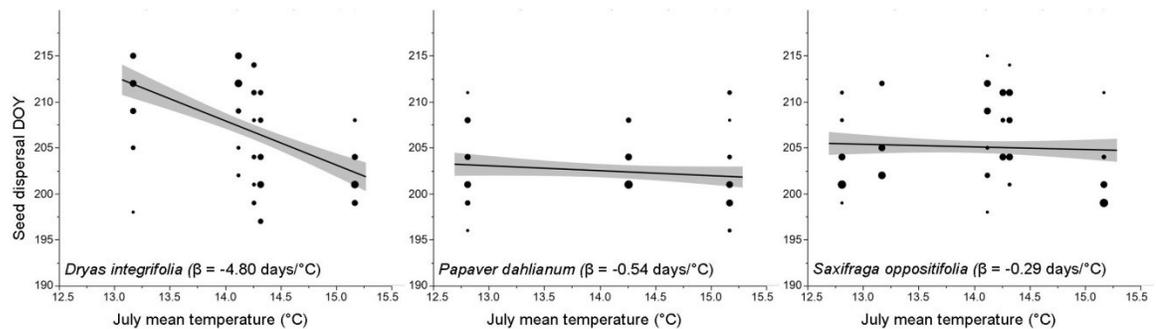


Figure 6.2. Species' seed dispersal time (day of year [DOY]) sensitivity to July mean temperature (β) showing how much earlier the species disperses seed with warmer July mean temperatures (Table 6.2). The size of the points on the graphs are proportional to the number of plants that peak flowered on the DOY and July mean temperature co-ordinate and the grey shading indicates the 95% confidence limit.

Interestingly, the warmest site was at the middle elevation (470 m.a.s.l.), the coldest site, as expected, was the highest site (784 m.a.s.l.) and all other sites were very close in GDD and were hence classified as intermediate (Figure 6.3). The warmest site is at the mid-elevation because Lake Hazen is ice covered until the end of July (Surdu et al., 2015) and hence sites closer to the lake were colder than those at middle elevations due to the cooling effect of the lake ice.

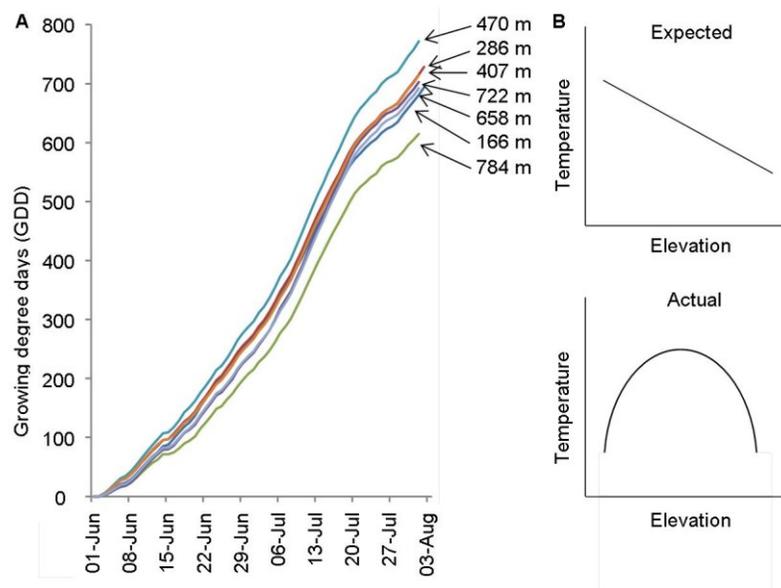


Figure 6.3. Growing degree days (GDD) for each elevation (1st June - 31st July 2015) (A). The inset graphs (B) illustrate an expected temperature gradient along an elevational gradient and the actual temperature gradient observed at Lake Hazen. The warmest site is at the mid elevation because Lake Hazen is ice covered until the end of July (Surdu et al. 2015) and hence sites closer to the lake are colder than those at the middle elevation while sites at the highest elevations are colder than those at middle elevations.

On average, plants at the coldest site/highest elevation required significantly fewer GDD to reach peak flower than conspecifics at the warmest and intermediate sites (Table 6.3, Figure 6.4). *Dryas integrifolia* plants required significantly fewer GDD to flower at

intermediate sites than at the warmest site. *Papaver dahlianum* and *Ranunculus sulphureus* plants required significantly fewer GDD at the coldest site than warmest and intermediate sites. *Saxifraga oppositifolia* and *S. tricuspidata* required significantly fewer GDD at the coldest and warmest site than at the intermediate sites. *Cassiope tetragona* plants were only monitored at the warmest site and intermediate sites and required no significantly different GDD at these two sites. *Alopecurus magellanicus* was only monitored at intermediate sites.

Table 6.3. Tukey-Kramer HSD ANOVA test for significant differences in mean growing degree days (GDD) required to reach peak flower between the coldest, intermediate (int,) and warmest sites (indicated by different letters) for each species and for all species combined.

Species	Mean GDD coldest site	Mean GDD int. sites	Mean GDD warmest site	q	P
<i>Cassiope tetragona</i>	-	320.84 (a)	304.94 (a)	1.98	0.0532
<i>Dryas integrifolia</i>	-	315.38 (a)	271.04 (b)	1.98	<.0001
<i>Papaver dahlianum</i>	306.41 (a)	371.08 (b)	405.51 (c)	2.38	0.0090
<i>Ranunculus sulphureus</i>	176.17 (a)	227.05 (b)	233.05 (b)	2.38	<.0001
<i>Saxifraga oppositifolia</i>	147.18 (a)	191.46 (b)	149.58 (a)	2.36	<.0001
<i>Saxifraga tricuspidata</i>	433.95 (a)	506.87 (b)	464.43 (a)	2.37	0.0008
All species combined	265.93 (a)	313.38 (b)	304.76 (b)	2.35	0.0064

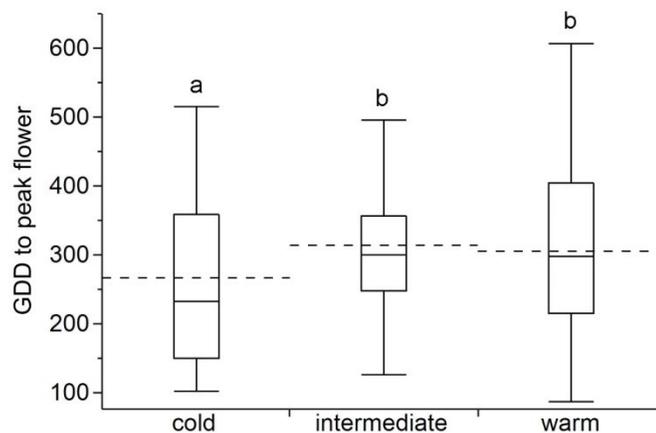


Figure 6.4. Growing degree days (GDD) required to reach peak flower of all seven species (Table 6.3) at the coldest, intermediate and warmest sites, showing that plants at the coldest site require significantly fewer GDD to reach peak flower than plants at the intermediate and warmest sites.

As expected *Saxifraga oppositifolia*, an early-spring-flowering species, requires the fewest mean GDD to reach peak flower (177°days) and *Saxifraga tricuspidata*, a late-summer-flowering species, requires the most GDD (478°days) (Table 6.4). *Alopecurus magellanicus* had the smallest range in GDD and *Papaver dahlianum* the greatest range in GDD.

Table 6.4. Maximum, minimum, range and mean growing degree days (GDD) required by a species to reach peak flower.

Species	Min.	Max.	Range	Mean	Std Dev	N
<i>Alopecurus magellanicus</i>	280.72	405.10	124.38	336.45	28.86	114
<i>Dryas integrifolia</i>	214.31	362.43	148.12	306.51	39.94	150
<i>Ranunculus sulphureus</i>	148.30	296.83	148.53	212.09	35.25	90
<i>Saxifraga oppositifolia</i>	86.78	299.03	212.25	177.02	35.80	179
<i>Cassiope tetragona</i>	197.63	416.10	218.47	317.64	40.33	149
<i>Saxifraga tricuspidata</i>	296.83	628.05	331.22	478.03	59.07	120
<i>Papaver dahlianum</i>	215.41	550.83	335.42	361.00	60.03	90

6.5 Discussion

The aim of this study was to use an elevational gradient as a proxy for climate change to determine the flowering and seed dispersal time sensitivity of seven Arctic species to temperature. For six of the seven species flowering times were sensitive to temperature and for one of three species seed dispersal time was sensitive to temperature. A long-term phenological monitoring study at Tanquary Fiord, Ellesmere Island, a location close to, and climatically and environmentally similar to the Lake Hazen study site, found a similar order of magnitude in flowering time temperature-sensitivity (elevation gradient versus long-term monitoring: -1.6 versus -1.8 days/°C for *Saxifraga oppositifolia* and -4.7 versus -2.3 days/°C for *Dryas integrifolia*) (Panchen and Gorelick, 2015). However, the substantial difference in absolute value for *Dryas integrifolia*

highlights the challenges in accurately measuring the phenological temperature-sensitivity and the potential for under- or over-estimating the sensitivity by the two approaches (Wolkovich et al., 2012). *Saxifraga oppositifolia* fruiting phenology was not sensitive to temperature while *Dryas integrifolia* fruiting phenology was sensitive to temperature in both the elevational gradient of this study at Lake Hazen and the above mentioned long-term monitoring study at Tanquary Fiord. This elevational gradient study at Lake Hazen found that *Cassiope tetragona* displayed flowering time sensitivity to temperature, while experimental warming studies indicate that this species' flowering and vegetative phenology is not sensitive to temperature (Molau, 1997; Khorsand Rosa et al., 2015). This difference in findings could be an indication of experimental warming underestimating phenological sensitivity (Wolkovich et al., 2012) or an artifact of variance in flowering time due to the month plus flowering duration of *Cassiope tetragona* (Panchen and Gorelick, 2016a).

Dryas integrifolia is a dominant species in the Arctic landscape (Gould, 1985; Soper and Powell, 1985; Edlund and Alt, 1989). *Dryas integrifolia* was also the species whose flowering time was most sensitive to temperature and the only species whose seed dispersal time was sensitive to temperature in the Lake Hazen elevational gradient study. In addition, other studies have shown *Dryas integrifolia* to be adaptable to different climatic and environmental conditions (Hart and Svoboda, 1994; Wookey et al., 1995). Hence, with its apparent climatic and environmental phenotypic plasticity and/or evolutionary adaptability, *Dryas integrifolia* is likely to remain a dominant species in the Arctic landscape.

The range among species in GDD required to reach peak flower was large (125 to 335°days), suggesting substantial plasticity in the time of flowering. However, this substantial variation might be expected if Arctic plant species are to be reproductively successful in a climate with great inter-annual variation in temperatures (Molau et al., 2005; Panchen and Gorelick, 2015, 2016b; Environment Canada, 2016). *Alopecurus magellanicus* had the smallest GDD range (125°days) probably because it only grows at Lake Hazen's intermediate temperature sites and not at the coldest or warmest sites. *Papaver dahlianum* showed no flowering or seed dispersal time sensitivity to temperature in this study but had the greatest range of GDD (335°days) and hence it is possible that this large variation in GDD masked detection of phenological temperature-sensitivity of *Papaver dahlianum*. The range of GDD to peak flower observed in *Papaver dahlianum* at Lake Hazen (215 – 515°days) was also greater than that of the closely related *Papaver radicum* observed at Alexandra Fiord (150 – 200°days) (Levesque et al., 1997), a similar polar oasis and close by on Ellesmere Island to Lake Hazen. However, the GDD measurements at Alexandra Fiord were to start, not peak, of flowering and hence would inevitably be smaller.

As might be expected, later-flowering species require more GDD to flower. Clearly, in a cold year, the late-flowering Arctic species that require more GDD to flower are less likely to flower or flower too late to produce seed compared to early-flowering species that require fewer GDD to flower. However, as temperatures become warmer due to climate change these late-flowering species may become more successful at flowering and producing seed. The late-flowering Arctic species are described as employing a seed risk strategy for reproductive success, i.e. producing many seeds but only in favourable

years while early-flowering species are described as employing a pollen risk strategy, producing fewer seeds but doing so in both favourable and unfavourable years (Molau, 1993a). Therefore, as the climate warms and the GDD are higher earlier in the year, late-flowering species such as *Saxifrage tricuspidata* may have a distinct advantage in reproductive success compared to early-flowering species such as *Saxifraga oppositifolia*.

This study showed that there were significant differences in the number of GDD required to reach peak flowering at the coldest versus warmest and/or intermediate sites. This suggests that plants at the coldest site might be evolutionarily adapted to the colder environment and initiate flowering with less heat input (Clausen et al., 1941; van Dijk et al., 1997; Weber and Schmid, 1998; Olsson and Ågren, 2002; Wagner and Simons, 2009).

In conclusion, this is a good news story for the Arctic plant species studied. They have the potential to respond to the warming temperatures of climate change and, as temperatures warm, the plants' potential for sexual reproductive success will likely increase from what is now a very low level, thus increasing the populations' genetic diversity (Müller et al., 2011).

7 Chapter: Conclusion

The overarching objective of this thesis was to study the reproductive phenological responses of Arctic plants to contemporary climate change. Chapter 2 showed that High Arctic species flower earlier or at the same time and for a shorter duration than their mid-Arctic conspecifics. Chapter 3 highlighted the dramatic year-to-year differences in flower abundance and the potential consequences for sexual reproductive success in a changing climate with pronounced weather extremes given the three plus years of favourable conditions required for sexual reproductive success. Chapters 4-6 used long-term phenology monitoring, historic phenology records and an elevation gradient to show that the vast majority of Arctic plant species studied are responsive to rising temperatures of climate change.

That Arctic plant reproductive phenology is sensitive to climate change is a good news story for Arctic plant communities where, currently, reproduction is predominantly vegetative (Chapin, 1992; Pielou, 1994). The responsiveness of Arctic plant species to warming temperatures and the accompanying lengthening of the short Arctic growing season could increase the potential for sexual reproductive success and genetic diversity of plant populations. Although, as Chapter 3 illustrates, this good news story could be tempered by increased climatic extremes. In addition, some species showed little or no reproductive phenological response to changes in temperature and hence could be of conservation concern (Primack, 2012). Species that showed little or no reproductive phenological temperature-sensitivity that are already uncommon in the landscape such as *Androsace septentrionalis* or *Erigeron compositus* are likely of more concern than

species such as *Chamerion latifolium*, *Papaver dahlianum* or *Saxifraga oppositifolia* that are common in the landscape.

Chapters 4 and 5 support the principle hypothesis of this thesis that fruiting phenology is advancing more than flowering phenology and mid- and late-summer-flowering species are advancing flowering times more than spring- or early-summer-flowering species. In addition, Chapters 4 and 5 also provide supporting evidence that Nunavut late summer, autumn and winter temperatures are rising the most. Temperature is a random variable because the thermometer only records the temperature at one exact location.

Three different methods were used in this thesis to determine the reproductive phenological temperature-sensitivity of a range of Arctic plant species, namely long-term phenological monitoring, phenological historical records (herbarium specimens, photographs and field observations) and an elevation gradient. While the methods all proved to be robust, they each predicted different magnitudes of response for a species. Thus, accurately enumerating the response for a species is a challenge and the variation in measured temperature-sensitivity is likely impacted by intraspecific phenological differences across latitudes, elevations and microclimates, inter-annual variation in temperature, and start and end year of the analysis (Clausen et al., 1941; Olsson and Ågren, 2002; Wagner and Simons, 2009; Baker et al., 2016). Perhaps a more realistic goal would be to predict and compare responses among different growth forms or reproductive strategies (Molau et al., 2005; Oberbauer et al., 2013; Khorsand Rosa et al., 2015) or among phylogenetic clades (Panchen et al., 2014). However, this would require

analyzing a much broader spectrum of Arctic species than included in this thesis, possibly through a meta-analysis.

There is great diversity in the reproductive phenological responses among Arctic plants species to climate change. Chapters 4, 5 and 6 indicate that mid-summer-flowering species have greater flowering time temperature-sensitivity than early- or late-flowering species. Chapters 5 and 6 suggested that these diverse responses will have implications for ecological communities such as altered community composition, plant competition and pollinator interactions. A future avenue of research, through modelling and field experiments, would be to investigate what those implications might be based on the relative responses of species in the community and ask whether that relative response will put a species at an advantage or disadvantage in the ecological community.

A common theme in Chapters 2, 5 and 6 was the suggestion that there is both phenotypic plasticity and evolutionary adaption at play in Arctic plant responses to climate change (Roy et al., 2015). Hence, future lines of enquiry could be to determine the relative importance of phenotypic plasticity versus evolutionary adaption in Arctic plant climate change responses using field experiments and controlled crosses or genetic analysis and knock out gene experiments (Anderson et al., 2012).

A number of journal reviewers of the papers included in this thesis questioned whether snow melt-out date or photoperiod could be the determining factor for time of flowering of Arctic plants. From Chapters 2 and 4-6, it is clear that temperature is a contributing factor in the time of flowering of most Arctic species and from Chapters 2 and 4, that snow melt-out date is less likely a contributing factor, particularly in polar deserts. In reality temperature, photoperiod and snow melt-out date are likely all

contributing factors depending on the species, latitude and climatic conditions (Heide et al., 1990; Bernier and Périlleux, 2005). Flowering time control is a complex process (Bernier and Périlleux, 2005) and would require considerable further study to fully disentangle the factors controlling Arctic plant flowering times and hence fully understand how flowering times will change with the temperature and precipitation shifts associated with climate change.

In summary, this thesis found that (i) Arctic plant flowering and fruiting times can respond to climate change possibly through phenotypic plasticity in the short term and evolutionary adaptation in the long term, (ii) late growing season phenology is advancing more than early growing season phenology reflecting the pattern of Arctic climate change where later growing season temperatures are rising more than early growing season temperatures and (iii) there is interspecific and inter-regional variation in flowering time temperature-sensitivity that could have implications for altered ecological community structure. These findings arose from the original objectives to determine (i) whether Nunavut plants are responding to climate change, (ii) the temperature-sensitivity of Nunavut Arctic plants and (iii) how the Nunavut climate is changing. However, perhaps the most significant contribution of this thesis is that these findings were consistent (i) at different spatial scales, from microclimates to across the 2.1 million km² of Nunavut, (ii) at different temporal scales from 20 years to 120 years and (iii) using three different methodologies of (a) long-term phenological monitoring, (b) herbarium, photographic and field observation records and (c) an elevation gradient as a proxy for climate change.

References

- ABU-ASAB, M., P. PETERSON, S. SHETLER, and S. ORLI. 2001. Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. *Biodiversity and Conservation* 10: 597–612.
- AERTS, R., J.H.C. CORNELISSEN, and 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 Ecology* 182: 65–77.
- AIKEN, S.G., M.J. DALLWITZ, L.L. CONSAUL, C.L. MCJANNET, R.L. BOLES, G.W. ARGUS, J.M. GILLET, ET AL. 2011. Flora of the Canadian Arctic Archipelago. Available at: <http://nature.ca/aaflora/data/index.htm>.
- ALATALO, J.M., and U. MOLAU. 1995. Effect of altitude on the sex ratio in populations of *Silene acaulis* (Caryophyllaceae). *Nordic Journal of Botany* 15: 251–256.
- ALATALO, J.M., and O. TOTLAND. 1997. Response to simulated climatic change in an alpine and subarctic pollen-risk strategist, *Silene acaulis*. *Global Change Biology* 3: 74–79.
- ALSOS, I.G., E. MULLER, and P.B. EIDASEN. 2013. Germinating seeds or bulbils in 87 of 113 tested Arctic species indicate potential for ex situ seed bank storage. *Polar Biology* 36: 819–830.
- AMAP. 2011. SWIPA 2011 executive summary: snow, water, ice and permafrost in the Arctic. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.
- AMAP. 2012a. Arctic climate issues 2011: changes in Arctic snow, water, ice and permafrost. SWIPA 2011 overview report. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.

- AMAP. 2012b. Climate change in the Arctic - a hot topic. SWIPA 2011: snow, water, ice and permafrost in the Arctic. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway.
- ANDERSON, J.T., D.W. INOUE, A.M. MCKINNEY, R.I. COLAUTTI, and T. MITCHELL-OLDS. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B-Biological Sciences* 279: 3843–3852.
- ARFT, A.M., M.D. WALKER, J. GUREVITCH, J.M. ALATALO, M.S. BRET-HARTE, M. DALE, M. DIEMER, ET AL. 1999. Responses of tundra plants to experimental warming: meta-analysis of the International Tundra Experiment. *Ecological Monographs* 69: 491–511.
- ATKINSON, D.E., and K. GAJEWSKI. 2002. High-resolution estimation of summer surface air temperature in the Canadian Arctic Archipelago. *Journal of Climate* 15: 3601–3614.
- BAKER, D.J., A.J. HARTLEY, S.H.M. BUTCHART, and S.G. WILLIS. 2016. Choice of baseline climate data impacts projected species' responses to climate change. *Global Change Biology* 22: 2392 – 2404.
- BALANDA, K.P., and H.L. MACGILLIVRAY. 1988. Kurtosis: A critical review. *The American Statistician* 42: 111–119.
- BARRETT, R.T.S., R.D. HOLLISTER, S.F. OBERBAUER, and C.E. TWEEDIE. 2015. Arctic plant responses to changing abiotic factors in northern Alaska. *American Journal of Botany* 102: 2020–2031.
- BARRY, R.G., and A.M. CARLETON. 2001. Synoptic and dynamic climatology. Routledge,

New York, NY.

- BEAUBIEN, E., and A. HAMANN. 2011. Spring flowering response to climate change between 1936 and 2006 in Alberta, Canada. *BioScience* 61: 514–524.
- BERNIER, G., and C. PÉRILLEUX. 2005. A physiological overview of the genetics of flowering time control. *Plant Biotechnology Journal* 3: 3–16.
- BERTIN, R.I. 2015. Climate change and flowering phenology in Worcester county, Massachusetts. *International Journal of Plant Sciences* 176: 107–119.
- BIENAU, M.J., M. KRÖNCKE, W.L. EISERHARDT, A. OTTE, B.J. GRAAE, D. HAGEN, A. MILBAU, ET AL. 2015. Synchronous flowering despite differences in snowmelt timing among habitats of *Empetrum hermaphroditum*. *Acta Oecologica* 69: 129–136.
- BJORKMAN, A.D., S.C. ELMENDORF, A.L. BEAMISH, M. VELLEND, and G.H.R. HENRY. 2015. Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Global Change Biology* 21: 4651–4661.
- BLINOVA, I., and F.-M. CHMIELEWSKI. 2015. Climatic warming above the Arctic Circle: are there trends in timing and length of the thermal growing season in Murmansk Region (Russia) between 1951 and 2012? *International Journal of Biometeorology* 59: 693–705.
- BLISS, L.C. 1971. Arctic and Alpine Plant Life Cycles. *Annual Review of Ecology and Systematics* 2: 405–438.
- BOCK, A., T.H. SPARKS, N. ESTRELLA, N. JEE, A. CASEBOW, C. SCHUNK, M. LEUCHNER, and A. MENZEL. 2014. Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey. *Global Change Biology* 20: 3508–3519.

- BORNER, A.P., K. KIELLAND, and M.D. WALKER. 2008. Effects of simulated climate change on plant phenology and nitrogen mineralization in Alaskan Arctic tundra. *Arctic, Antarctic, and Alpine Research* 40: 27–38.
- BRADLEY, N.L., A.C. LEOPOLD, J. ROSS, and H. WELLINGTON. 1999. Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the United States of America* 96: 9701–9704.
- BURN, C.R., and S. V KOKELJ. 2009. The environment and permafrost of the Mackenzie Delta area. *Permafrost and Periglacial Processes* 20: 83–105.
- BURN, C.R., and Y. ZHANG. 2009. Permafrost and climate change at Herschel Island (Qikiqtaruk), Yukon Territory, Canada. *Journal of Geophysical Research-Earth Surface* 114: 1–16.
- CADIEUX, M.-C., G. GAUTHIER, C.A. GAGNON, E. LÉVESQUE, J. BÊTY, and D. BERTEAUX. 2008. Monitoring the environmental and ecological impacts of climate change on Bylot Island, Sirmilik National Park 2004-2008 final report. Quebec, QC, Canada.
- CALINGER, K.M., S. QUEENBOROUGH, and P.S. CURTIS. 2013. Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America. *Ecology Letters* 16: 1037–1044.
- CALLAGHAN, T. V. 2005. Arctic tundra and polar desert ecosystems. In C. Symon, L. Arris, and B. Heal [eds.], *Arctic Climate Impact Assessment*, 243–352. Cambridge University Press, Cambridge, UK.
- CANADIAN ICE SERVICE. 2002. *Sea Ice Climatic Atlas: Northern Canadian Waters 1971-2000*. Canadian Ice Service, Ottawa, ON, Canada.
- CARADONNA, P.J., A.M. ILER, and D.W. INOUE. 2014. Shifts in flowering phenology

- reshape a subalpine plant community. *Proceedings of the National Academy of Sciences of the United States of America* 111: 4916–4921.
- CAYAN, D.R., S.A. KAMMERDIENER, M.D. DETTINGER, J.M. CAPRIO, and D.H. PETERSON. 2001. Changes in the onset of spring in the western United States. *Bulletin of the American Meteorological Society* 82: 399–415.
- CHAPIN, F.S. 1992. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego, CA.
- CHMIELEWSKI, F.-M., and T. RÖTZER. 2001. Response of tree phenology to climate change across Europe. *Agricultural and Forest Meteorology* 108: 101–112.
- CLAUSEN, J., D.D. KECK, and W.M. HIESEY. 1941. Regional differentiation in plant species. *American Naturalist* 75: 231–250.
- COOK, B.I., E.M. WOLKOVICH, T.J. DAVIES, T.R. AULT, J.L. BETANCOURT, J.M. ALLEN, K. BOLMGREN, ET AL. 2012a. Sensitivity of spring phenology to warming across temporal and spatial climate gradients in two independent databases. *Ecosystems* 15: 1283–1294.
- COOK, B.I., E.M. WOLKOVICH, and C. PARMESAN. 2012b. Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences of the United States of America* 109: 9000–9005.
- COPLAND, L., D.R. MUELLER, and L. WEIR. 2007. Rapid loss of the Ayles Ice Shelf, Ellesmere Island, Canada. *Geophysical Research Letters* 34: 1–6.
- CRAWFORD, R.M.M., H.M. CHAPMAN, and L.C. SMITH. 2009. Adaptation to variation in growing season length in Arctic populations of *Saxifraga oppositifolia* L. *Botanical Journal of Scotland* 47: 177–192.

- CRIMMINS, T., C.D. BERTELSEN, and M. CRIMMINS. 2014. Within-season flowering interruptions are common in the water-limited Sky Islands. *International Journal of Biometeorology* 58: 419–426.
- CULLEY, T.M. 2013. Why vouchers matter in botanical research. *Applications in Plant Sciences* 1: 1300076.
- DAVIES, T.J., E.M. WOLKOVICH, N.J.B. KRAFT, N. SALAMIN, J.M. ALLEN, T.R. AULT, J.L. BETANCOURT, ET AL. 2013. Phylogenetic conservatism in plant phenology. *Journal of Ecology* 101: 1520–1530.
- DAVIS, C.C., C.G. WILLIS, B. CONNOLLY, C. KELLY, and A.M. ELLISON. 2015. Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms. *American Journal of Botany* 102: 1599–1609.
- DAVIS, C.C., C.G. WILLIS, and R.B.M.-R. PRIMACK A.J. 2010. The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3201–3213.
- VAN DIJK, H., P. BOUDRY, H. MCCOMBRE, and P. VERNET. 1997. Flowering time in wild beet (*Beta vulgaris* ssp. *maritima*) along a latitudinal cline. *Acta Oecologica* 18: 47–60.
- DISKIN, E., H. PROCTOR, M. JEBB, T. SPARKS, and A. DONNELLY. 2012. The phenology of *Rubus fruticosus* in Ireland: herbarium specimens provide evidence for the response of phenophases to temperature, with implications for climate warming. *International Journal of Biometeorology* 56: 1103–1111.

- EASTERLING, D.R., T.R. KARL, K.P. GALLO, D.A. ROBINSON, K.E. TRENBERTH, and A. DAI. 2000a. Observed climate variability and change of relevance to the biosphere. *Journal of Geophysical Research* 105: 20101–20114.
- EASTERLING, D.R., G.A. MEEHL, C. PARMESAN, S.A. CHANGNON, T.R. KARL, and L.O. MEARNS. 2000b. Climate extremes: observations, modeling, and impacts. *Science* 289: 2068–2074.
- EDLUND, S.A., and B.T. ALT. 1989. Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada. *Arctic* 42: 3–23.
- ELLEBJERG, S.M., M.P. TAMSTORF, L. ILLERIS, A. MICHELSEN, and B.U. HANSEN. 2008. Inter-annual variability and controls of plant phenology and productivity at Zackenberg. *Advances in Ecological Research* 40: 249–273.
- ELLWOOD, E., S. PLAYFAIR, C. POLGAR, and R. PRIMACK. 2014. Cranberry flowering times and climate change in southern Massachusetts. *International Journal of Biometeorology* 58: 1693–1697.
- ELVEN, R. 2003. Annotated checklist of the Pan-Arctic flora (PAF) vascular plants. Available at: <http://nhm2.uio.no/paf/>.
- ENVIRONMENT CANADA. 2016. National climate data and information archive. Available at: http://climate.weather.gc.ca/index_e.html.
- ERIKSEN, B., U. MOLAU, and M. SVENSSON. 1993. Reproductive strategies in two Arctic *Pedicularis* species (Scrophulariaceae). *Ecography* 16: 154–166.
- EUSKIRCHEN, E.S., T.B. CARMAN, and A.D. MCGUIRE. 2014. Changes in the structure and function of northern Alaskan ecosystems when considering variable leaf-out

- times across groupings of species in a dynamic vegetation model. *Global Change Biology* 20: 963–978.
- FENECH, A. 2013. Hot off the press – the most recent scenarios of future climate change from the 40 global climate models used in the fifth assessment report (AR5) of the Intergovernmental Panel on Climate Change (IPCC). *NWRC Seminar Series*.
- FITTER, A.H., R.S.R. FITTER, I.T.B. HARRIS, and M.H. WILLIAMSON. 1995. Relationships between first flowering date and temperature in the flora of a locality in central England. *Functional Ecology* 9: 55–60.
- FLETCHER, R.J., and G.S. YOUNG. 1970. Climate of Arctic Canada in maps. Boreal Institute for Northern Studies, Edmonton, AB, Canada.
- FOX, J.F., and G.C. STEVENS. 1991. Costs of reproduction in a willow - experimental responses vs natural variation. *Ecology* 72: 1013–1023.
- FRASER, D.B. 1983. Climate of the Northwestern Baffin Bay and Lancaster Sound. Department of Indian Affairs and Northern Development, Ottawa, ON, Canada.
- FREI, E.R., J. GHAZOUL, P. MATTER, M. HEGGLI, and A.R. PLUESS. 2014. Plant population differentiation and climate change: responses of grassland species along an elevational gradient. *Global Change Biology* 20: 441–455.
- FURGAL, C., and T.D. PROWSE. 2007. Northern Canada. In D. S. Lemmen, F. J. Warren, and J. Lacroix [eds.], From impacts to adaptation: Canada in a changing climate, 57–118. Natural Resources Canada, Ottawa, ON, Canada.
- GALLAGHER, R. V, M.R. LEISHMAN, and L. HUGHES. 2009. Phenological trends among Australian alpine species: using herbarium records to identify climate-change indicators. *Australian Journal of Botany* 57: 1–9.

- GALLINAT, A.S., R.B. PRIMACK, and D.L. WAGNER. 2015. Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution* 30: 169–176.
- GE, Q., H. WANG, T. RUTISHAUSER, and J. DAI. 2014. Phenological response to climate change in China: a meta-analysis. *Global Change Biology* 21: 265–274.
- GORDO, O., and J.J. SANZ. 2010. Impact of climate change on plant phenology in Mediterranean ecosystems. *Global Change Biology* 16: 1082–1106.
- GOULD, A.J. 1985. Plant communities of the Lake Hazen area, Ellesmere Island, N.W.T. Ph.D. dissertation, University of Toronto, Toronto, Canada.
- HARE, K. 1997. Canada's climate: an overall perspective. In W. R. Rouse, W. G. Bailey, and T. R. Oke [eds.], *The surface climates of Canada*, 3–20. McGill-Queen's University Press, Montreal, QC, Canada.
- HART, G.T., and J. SVOBODA. 1994. Autecology of *Dryas integrifolia* in Alexandria Fiord lowland habitat. In J. Svoboda, and B. Freedman [eds.], *Ecology of a polar oasis: Alexandria Fiord, Ellesmere Island, Canada*, 145–156. Captus Press, North York, ON.
- HART, R., J. SALICK, S. RANJITKAR, and J. XU. 2014. Herbarium specimens show contrasting phenological responses to Himalayan climate. *Proceedings of the National Academy of Sciences of the United States of America* 111: 10615–10619.
- HARTMANN, D.L., A.M.G. KLEIN TANK, M. RUSTICUCCI, L.V. ALEXANDER, S. BRÖNNIMANN, Y. CHARABI, F.J. DENTENER, ET AL. 2013. Observations: Atmosphere and Surface. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, et al. [eds.], *Climate Change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the*

- Intergovernmental Panel on Climate, 159–254. Cambridge University Press, Cambridge, United Kingdom; New York, NY.
- HEALY, C., and L.J. GILLESPIE. 2004. A systematic analysis of the alpine saxifrage complex (Saxifragaceae) in the Canadian Arctic Islands using morphology and chloroplast DNA data. *Canadian Field-Naturalist* 118: 326–340.
- HEGLAND, S.J., A. NIELSEN, A. LÁZARO, A.-L. BJERKNES, and Ø. TOTLAND. 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12: 184–195.
- HEIDE, O.M. 2005. Ecotypic variation among European Arctic and alpine populations of *Oxyria digyna*. 37: 233–238.
- HEIDE, O.M., K. PEDERSEN, and E. DAHL. 1990. Environmental control of flowering and morphology in the high-arctic *Cerastium regelii*, and the taxonomic status of *C. jenisejense*. *Nordic Journal of Botany* 10: 141–147.
- HENRY, G.H.R., and U. MOLAU. 1997. Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology* 3: 1–9.
- HERTZMAN, O. 1997. Oceans and the coastal zone. In W. R. Rouse, W. G. Bailey, and T. R. Oke [eds.], *The surface climates of Canada*, 101–109. McGill-Queen's University Press, Montreal, QC, Canada.
- HOLOPAINEN, J., S. HELAMA, H. LAPPALAINEN, and H. GREGOW. 2013. Plant phenological records in northern Finland since the 18th century as retrieved from databases, archives and diaries for biometeorological research. *International Journal of Biometeorology* 57: 423–435.
- HOLWAY, J.G., and R.T. WARD. 1965. Phenology of alpine plants in northern Colorado.

- Ecology* 46: 73–83.
- HØYE, T.T., S.M. ELLEBJERG, and M. PHILIPP. 2007a. The impact of climate on flowering in the High Arctic - the case of *Dryas* in a hybrid zone. *Arctic, Antarctic, and Alpine Research* 39: 412–421.
- HØYE, T.T., E. POST, H. MELTOFTE, N.M. SCHMIDT, and M.C. FORCHHAMMER. 2007b. Rapid advancement of spring in the High Arctic. *Current Biology* 17: R449–R451.
- HØYE, T.T., E. POST, N.M. SCHMIDT, K. TRØJELSGAARD, and M.C. FORCHHAMMER. 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nature Climate Change* 3: 759–763.
- HÜLBER, K., M. WINKLER, and G. GRABHERR. 2010. Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species. *Functional Ecology* 24: 245–252.
- ILER, A.M., T.T. HOYE, D.W. INOUE, and N.M. SCHMIDT. 2013a. Long-term trends mask variation in the direction and magnitude of short-term phenological shifts. *American Journal of Botany* 100: 1398–1406.
- ILER, A.M., T.T. HOYE, D.W. INOUE, and N.M. SCHMIDT. 2013b. Nonlinear flowering responses to climate: are species approaching their limits of phenological change? *Philosophical Transactions of the Royal Society B-Biological Sciences* 368: .
- INOUE, D.W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89: 353–362.
- INOUE, D.W., and A.D. MCGUIRE. 1991. Effects of snowpack on timing and abundance of flowering in *Delphinium nelsonii* (Ranunculaceae): Implications for climate change. *American Journal of Botany* 78: 997–1001.

- INOUE, D.W., F. SAAVEDRA, and W. LEE-YANG. 2003. Environmental influences on the phenology and abundance of flowering by *Androsace septentrionalis* (Primulaceae). *American Journal of Botany* 90: 905–910.
- JONES, M.H., C. BAY, and U. NORDENHALL. 1997. Effects of experimental warming on arctic willows (*Salix* spp.): a comparison of responses from the Canadian High Arctic, Alaskan Arctic, and Swedish Subarctic. *Global Change Biology* 3: 55–60.
- KELLER, F., and C. KÖRNER. 2003. The role of photoperiodism in Alpine plant development. *Arctic, Antarctic, and Alpine Research* 35: 361–368.
- KEVAN, P.G. 1972. Insect Pollination of High Arctic Flowers. *Journal of Ecology* 60: 831–847.
- KHORSAND ROSA, R., S.F. OBERBAUER, G. STARR, I. PARKER LA PUMA, E. POP, L. AHLQUIST, and T. BALDWIN. 2015. Plant phenological responses to a long-term experimental extension of growing season and soil warming in the tussock tundra of Alaska. *Global Change Biology* 21: 4520–4532.
- KIMBALL, K.D., M.L. DAVIS, D.M. WEIHRAUCH, G.L.D. MURRAY, and K. RANCOURT. 2014. Limited alpine climatic warming and modeled phenology advancement for three alpine species in the northeast United States. *American Journal of Botany* 101: 1437–1446.
- KLADY, R.A., G.H.R. HENRY, and V. LEMAY. 2011. Changes in High Arctic tundra plant reproduction in response to long-term experimental warming. *Global Change Biology* 17: 1611–1624.
- KREMERS, K.S., R.D. HOLLISTER, and S.F. OBERBAUER. 2015. Diminished response of arctic plants to warming over time. *PLoS One* 10: e0116586.

- KUDO, G., and A.S. HIRAO. 2006. Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts. *Population Ecology* 48: 49–58.
- LARL, I., and J. WAGNER. 2006. Timing of reproductive and vegetative development in *Saxifraga oppositifolia* in an alpine and a subnival climate. *Plant Biology* 8: 155–66.
- LAVOIE, C., and D. LACHANCE. 2006. A new herbarium-based method for reconstructing the phenology of plant species across large areas. *American Journal of Botany* 93: 512–516.
- LEATHERS, D.J., M.L. MALIN, D.B. KLUVER, G.R. HENDERSON, and T.A. BOGART. 2008. Hydroclimatic variability across the Susquehanna River Basin, USA, since the 17th century. *International Journal of Climatology* 28: 1615–1626.
- LEDNEVA, A., A.J. MILLER-RUSHING, R.B. PRIMACK, and C. IMBRES. 2004. Climate change as reflected in a naturalist's diary, Middleborough, Massachusetts. *Wilson Bulletin* 116: 224–231.
- LEGAULT, G., and M. CUSA. 2015. Temperature and delayed snowmelt jointly affect the vegetative and reproductive phenologies of four sub-Arctic plants. *Polar Biology* 38: 1701–1711.
- LESSARD-THERRIEN, M., T.J. DAVIES, and K. BOLMGREN. 2013. A phylogenetic comparative study of flowering phenology along an elevational gradient in the Canadian subarctic. *International Journal of Biometeorology* 58: 455–462.
- LEVESQUE, E., G.H.R. HENRY, and J. SVOBODA. 1997. Phenological and growth responses of *Papaver radicum* along altitudinal gradients in the Canadian High Arctic. *Global Change Biology* 3: 125–145.

- MACGILLIVRAY, F., I.L. HUDSON, and A.J. LOWE. 2010. Herbarium collections and photographic images: alternative data sources for phenological research. *In* I. L. Hudson, and M. R. Keatley [eds.], Phenological research: Methods for environmental and climate change analysis, 425–461. Springer, Netherlands.
- MALLORY, C., and S. AIKEN. 2012. Common plants of Nunavut. Inhabit Media, Toronto, Canada.
- MAXWELL, B. 1997. Responding to global climate change in Canada's Arctic. Environment Canada, Toronto, ON, Canada.
- MAZER, S.J., S.E. TRAVERS, B.I. COOK, T.J. DAVIES, K. BOLMGREN, N.J.B. KRAFT, N. SALAMIN, and D.W. INOUE. 2013. Flowering date of taxonomic families predicts phenological sensitivity to temperature: Implications for forecasting the effects of climate change on unstudied taxa. *American Journal of Botany* 100: 1381–1397.
- MCBEAN, G. 2004. Arctic climate: past and present. *In* S. Hassol [ed.], Impacts of a warming Arctic: Arctic climate impact assessment, 21–60. Cambridge University Press, Cambridge, U.K.
- MCKINNEY, A.M., P.J. CARADONNA, D.W. INOUE, W.A. BARR, C.D. BERTELSEN, and N.M. WASER. 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology* 93: 1987–1993.
- MENNE, M.J., J. WILLIAMS C.N., and R.S. VOSE. 2010. Long term daily and monthly climate records from stations across the contiguous United States. Available at: <http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html>.
- MENZEL, A. 2000. Trends in phenological phases in Europe between 1951 and 1996. *International Journal of Biometeorology* 44: 76–81.

- MENZEL, A., and P. FABIAN. 1999. Growing season extended in Europe. *Nature* 397: 659.
- MENZEL, A., T.H. SPARKS, N. ESTRELLA, E. KOCH, A. AASA, R. AHAS, K. ALM-KUBLER, ET AL. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12: 1969–1976.
- MILLER-RUSHING, A., and R.B. PRIMACK. 2008. Global warming and flowering times in Thoreau's Concord: a community perspective. *Ecology* 89: 332–341.
- MILLER-RUSHING, A.J., D.W. INOUE, and R.B. PRIMACK. 2008. How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *Journal of Ecology* 96: 1289–1296.
- MILLER-RUSHING, A.J., R.B. PRIMACK, D. PRIMACK, and S. MUKUNDA. 2006. Photographs and herbarium specimens as tools to document phenological changes in response to global warming. *American Journal of Botany* 93: 1667–1674.
- MOLAU, U. 1993a. Relationships between flowering phenology and life history strategies in tundra plants. *Arctic and Alpine Research* 25: 391–402.
- MOLAU, U. 1993b. Reproductive ecology of the three Nordic *Pinguicula* species (Lentibulariaceae). *Nordic Journal of Botany* 13: 149–157.
- 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 Biology* 3: 97–107.
- MOLAU, U. 2001. Tundra plant responses to experimental and natural temperature changes. *Memoirs of National Institute of Polar Research* 54: 445–466.
- MOLAU, U., and P. MØLGAARD. 1996. ITEX Manual. Danish Polar Centre, Denmark.
- MOLAU, U., U. NORDENHÅLL, and B. ERIKSEN. 2005. Onset of flowering and climate

- variability in an alpine landscape: a 10-year study from Swedish Lapland. *American Journal of Botany* 92: 422–31.
- MOONEY, H.A., and W.D. BILLINGS. 1960. The annual carbohydrate cycle of alpine plants as related to growth. *American Journal of Botany* 47: 594–598.
- MUELLER, D.R., W.F. VINCENT, and M.O. JEFFRIES. 2003. Ice shelf break-up and ecosystem loss in the Canadian High Arctic. *Eos - Transactions of the American Geophysical Union* 84: 548.
- MÜLLER, E., E.J. COOPER, and I.G. ALSOS. 2011. Germinability of arctic plants is high in perceived optimal conditions but low in the field. *Botany-Botanique* 89: 337–348.
- MUNSON, S.M., and A.A. SHER. 2015. Long-term shifts in the phenology of rare and endemic Rocky Mountain plants. *American Journal of Botany* 102: 1268–1276.
- NAOYA, W. 1999. Factors affecting the seed-setting success of *Dryas octopetala* in front of Brøggerbreen (Brøgger Glacier) in the High Arctic, Ny-Ålesund, Svalbard. *Polar Research* 18: 261–268.
- NEIL, K.L., L. LANDRUM, and J. WU. 2010. Effects of urbanization on flowering phenology in the metropolitan phoenix region of USA: findings from herbarium records. *Journal of Arid Environments* 74: 440–444.
- OBERBAUER, S.F., S.C. ELMENDORF, T.G. TROXLER, R.D. HOLLISTER, A. V ROCHA, M.S. BRET-HARTE, M.A. DAWES, ET AL. 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 368: 20120481.
- OLSSON, K., and J. ÅGREN. 2002. Latitudinal population differentiation in phenology, life

- history and flower morphology in the perennial herb *Lythrum salicaria*. *Journal of Evolutionary Biology* 15: 983–996.
- OVERPECK, J., K. HUGHEN, D. HARDY, R. BRADLEY, R. CASE, M. DOUGLAS, B. FINNEY, ET AL. 1997. Arctic environmental change of the last four centuries. *Science* 278: 1251–1256.
- PANCHEN, Z.A. 2016. Arctic plants produce vastly different numbers of flowers in three contrasting years at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut, Canada. *Canadian Field-Naturalist* 130: 56–63.
- PANCHEN, Z.A., and R. GORELICK. 2016a. Canadian Arctic Archipelago conspecifics flower earlier in the High Arctic than the mid-Arctic. *International Journal of Plant Sciences* In Press: .
- PANCHEN, Z.A., and 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 Science* 1: 45–58.
- PANCHEN, Z.A., and R. GORELICK. 2016b. Prediction of Arctic plant phenological sensitivity to climate change from historical records. *In review*.
- PANCHEN, Z.A., R.B. PRIMACK, T. ANIŠKO, and R.E. LYONS. 2012. Herbarium specimens, photographs, and field observations show Philadelphia area plants are responding to climate change. *American Journal of Botany* 99: 751–756.
- PANCHEN, Z.A., R.B. PRIMACK, A.S. GALLINAT, B. NORDT, A.-D. STEVENS, Y. DU, and R. FAHEY. 2015. Substantial variation in leaf senescence times among 1360 temperate woody plant species: implications for phenology and ecosystem processes. *Annals of Botany* 116: 865–73.

- PANCHEN, Z.A., R.B. PRIMACK, B. NORDT, E.R. ELLWOOD, A.D. STEVENS, S.S. RENNER, C.G. WILLIS, ET AL. 2014. Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. *New Phytologist* 203: 1208–1219.
- PARK, I.W., and M.D. SCHWARTZ. 2015. Long-term herbarium records reveal temperature-dependent changes in flowering phenology in the southeastern USA. *International Journal of Biometeorology* 59: 347–355.
- PARKS CANADA. 2002. QNP ITEX field protocol. Nunavut Field Unit, Parks Canada.
- PETRAGLIA, A., M. TOMASELLI, M. PETIT BON, N. DELNEVO, G. CHIARI, and M. CARBOGNANI. 2014. Responses of flowering phenology of snowbed plants to an experimentally imposed extreme advanced snowmelt. *Plant Ecology* 215: 759–768.
- PIELOU, E.C. 1994. A naturalist's guide to the Arctic. University of Chicago Press, Chicago, IL.
- PORSILD, A.E., and W.J. CODY. 1980. Vascular plants of continental Northwest Territories, Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, ON Canada.
- PREVÉY, J., C. RIXEN, R. HOLLISTER, G. HENRY, J. WELKER, U. MOLAU, E. LEVESQUE, ET AL. 2014. Flowering time and historical climate help explain phenological responses of arctic and alpine plants to climate change. *In* International Arctic Change 2014 Conference, 155–156.
- PRIMACK, D., C. IMBRES, R.B. PRIMACK, A.J. MILLER-RUSHING, and P. DEL TREDICI. 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany* 91: 1260–1264.

- PRIMACK, R.B. 2012. A primer of conservation biology. 5th ed. Sinauer Associates, Sunderland, MA.
- PRIMACK, R.B. 2003. The special role of historical plant records in monitoring the impact of climate change. *Arnoldia* 62: 12–15.
- PRIMACK, R.B., and A.J. MILLER-RUSHING. 2009. The role of botanical gardens in climate change research. *New Phytologist* 182: 303–313.
- PRZYBYLAK, R. 2003. The climate of the Arctic. Kluwer Academic Publishers, Boston, MA.
- RAILLARD, M. 1999. Plant phenology monitoring protocol. Western Arctic Field Unit, Parks Canada.
- RANJITKAR, S., E. LUEDELING, K. SHRESTHA, K. GUAN, and J. XU. 2013. Flowering phenology of tree rhododendron along an elevation gradient in two sites in the Eastern Himalayas. *International Journal of Biometeorology* 57: 225–240.
- RATHCKE, B., and E.P. LACEY. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16: 179–214.
- REID, P.C., R.E. HARI, G. BEAUGRAND, D.M. LIVINGSTONE, C. MARTY, D. STRAILE, J. BARICHIVICH, ET AL. 2015. Global impacts of the 1980s regime shift. *Global Change Biology* 22: 682–703.
- ROBBIRT, K.M., A.J. DAVY, M.J. HUTCHINGS, and D.L. ROBERTS. 2010. Validation of biological collections as a source of phenological data for use in climate change studies: a case study with the orchid *Ophrys sphegodes*. *Journal of Ecology* 99: 235–241.
- ROSSI, S. 2015. Local adaptations and climate change: converging sensitivity of bud

- break in black spruce provenances. *International Journal of Biometeorology* 59: 827–35.
- ROY, D.B., T.H. OLIVER, M.S. BOTHAM, B. BECKMANN, T. BRERETON, R.L.H. DENNIS, C. HARROWER, ET AL. 2015. Similarities in butterfly emergence dates among populations suggest local adaptation to climate. *Global Change Biology* 21: 3313–3322.
- RUMPF, L., F. COATES, and J.W. MORGAN. 2010. Biological indicators of climate change: evidence from long-term flowering records of plants along the Victorian coast, Australia. *Australian Journal of Botany* 58: 428–439.
- RYBCZYNSKI, N., J. GOSSE, and M. BUCKLEY. 2013. Mid-Pliocene warm-period deposits in the High Arctic yield insight into camel evolution. *Nature Communications* 4: 1550.
- SAVILE, D.B.O. 1964. General ecology and vascular plants of the Hazen Camp area. *Arctic* 17: 237–258.
- SCHWARTZ, M.D. 1994. Monitoring global change with phenology: the case of the spring green wave. *International Journal of Biometeorology* 38: 18–22.
- SEMENCHUK, P.R., B. ELBERLING, and E.J. COOPER. 2013. Snow cover and extreme winter warming events control flower abundance of some, but not all species in High Arctic Svalbard. *Ecology and Evolution* 3: 2586–99.
- SHARP, M., D.O. BURGESS, F. CAWKWELL, L. COPLAND, J.A. DAVIS, E.K. DOWDESWELL, J.A. DOWDESWELL, ET AL. 2014. Remote sensing of recent glacier changes in the Canadian Arctic. In J. S. Kargel, G. J. Leonard, M. P. Bishop, A. Kääb, and B. H. Raup [eds.], *Global land ice measurements from space*, 205–228. Springer, Berlin,

Heidelberg, Germany.

SHERRY, R.A., X. ZHOU, S. GU, J.A. ARNONE, D.S. SCHIMEL, P.S. VERBURG, L.L.

WALLACE, and Y. LUO. 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of the United States of America* 104: 198–202.

SOPER, J.H., and J.M. POWELL. 1985. Botanical studies in the Lake Hazen region, Northern Ellesmere Island, Northwest Territories, Canada. *Publications in Natural Science* 5: 1–67.

SØRENSEN, T.J. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. Universitets Annekset, Denmark.

SPRINGATE, D.A., and P.X. KOVER. 2014. Plant responses to elevated temperatures: a field study on phenological sensitivity and fitness responses to simulated climate warming. *Global Change Biology* 20: 456–465.

STENSTRÖM, A. 1999. Sexual reproductive ecology of *Carex bigelowii*, an Arctic-Alpine sedge. *Ecography* 22: 305–313.

STENSTRÖM, A., and I.S. JÓNSDÓTTIR. 2004. Effects of simulated climate change on phenology and life history traits in *Carex bigelowii*. *Nordic Journal of Botany* 24: 355–371.

STENSTRÖM, M., F. GUGERLI, and G.H.R. HENRY. 1997. Response of *Saxifraga oppositifolia* L. to simulated climate change at three contrasting latitudes. *Global Change Biology* 3: 44–54.

STENSTRÖM, M., and U. MOLAU. 1992. Reproductive ecology of *Saxifraga oppositifolia*: phenology, mating system, and reproductive success. *Arctic and Alpine Research*

24: 337–343.

- STOCKER, T.F., D. QIN, G.-K. PLATTNER, L.V. ALEXANDER, S.K. ALLEN, N.L. BINDOFF, F.-M. BRÉON, ET AL. 2013. Technical Summary. *In* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, et al. [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*, 33–115. Cambridge University Press, Cambridge, U.K.; New York, NY.
- SURDU, C.M., C.R. DUGUAY, and D. FERNÁNDEZ PRIETO. 2015. Evidence of recent changes in the ice regime of lakes in the Canadian High Arctic from spaceborne satellite observations. *The Cryosphere Discussions* 9: 6223–6274.
- SVOBODA, J., and B. FREEDMAN. 1994. Ecology of a polar oasis: Alexandra Fiord, Ellesmere Island, Canada. Captus Press, North York, ON.
- TEERI, J.A. 1976. Phytotron analysis of a photoperiodic response in a High Arctic plant species. *Ecology* 57: 374–379.
- THOMPSON, W. 1994. Climate. *In* Parks Canada [ed.], *Resource description and analysis: Ellesmere Island, National Park Reserve*, 1–78. National Resource Conservation Section, Prairie and Northern Region, Parks Canada, Department of Canadian Heritage, Winnipeg, MB, Canada.
- THÓRHALLSDÓTTIR, T.E. 1998. Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. *Oecologia* 114: 43–49.
- THROOP, J.L., S.L. SMITH, and A.G. LEWKOWICZ. 2010. Observed recent changes in climate and permafrost temperatures at four sites in northern Canada. *In* GEO2010, 63rd Canadian Geotechnical Conference and 6th Canadian Permafrost Conference,

- 1265–1272. Calgary, AB, Canada.
- TOTLAND, Ø., and J. ALATALO. 2002. Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis*. *Oecologia* 133: 168–175.
- VAN VLIET, A.J.H., W.A. BRON, S. MULDER, W. VAN DER SLIKKE, and B. ODE. 2014. Observed climate-induced changes in plant phenology in the Netherlands. *Regional Environmental Change* 14: 997–1008.
- WAGNER, I., and A.M. SIMONS. 2009. Divergence among Arctic and alpine populations of the annual, *Koenigia islandica*: morphology, life-history, and phenology. *Ecography* 32: 114–122.
- WEBER, E., and B. SCHMID. 1998. Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. *American Journal of Botany* 85: 1110–1121.
- WELKER, J.M., U. MOLAU, A.N. PARSONS, C.H. ROBINSON, and P.A. WOOKEY. 1997. Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. *Global Change Biology* 3: 61–73.
- WHEELER, H.C., T.T. HØYE, N.M. SCHMIDT, J.-C. SVENNING, and M.C. FORCHHAMMER. 2015. Phenological mismatch with abiotic conditions - implications for flowering in Arctic plants. *Ecology* 96: 775–787.
- WILLIS, C.G., J.B. LOSOS, C.C. DAVIS, A. MILLER-RUSHING, B.R. RUHFEL, and R.B. PRIMACK. 2010. Favorable climate change response explains non-native species' success in Thoreau's Woods. *PLoS One* 5: 1–5.
- WILLIS, C.G., A. MILLER-RUSHING, C.C. DAVIS, B. RUHFEL, and R.B. PRIMACK. 2008.

- Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences of the United States of America* 105: 17029–17033.
- WOLFE, D.W., M.D. SCHWARTZ, A.N. LAKSO, Y. OTSUKI, R.M. POOL, and N.J. SHAULIS. 2005. Climate change and shifts in spring phenology of three horticultural woody perennials in northeastern USA. *International Journal of Biometeorology* 49: 303–309.
- WOLKOVICH, E.M., B.I. COOK, J.M. ALLEN, T.M. CRIMMINS, J.L. BETANCOURT, S.E. TRAVERS, S. PAU, ET AL. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485: 494–497.
- WOLKOVICH, E.M., T.J. DAVIES, H. SCHAEFER, E.E. CLELAND, B.I. COOK, S.E. TRAVERS, C.G. WILLIS, and C.C. DAVIS. 2013. Temperature-Dependent Shifts in Phenology Contribute to the Success of Exotic Species with Climate Change. *American Journal of Botany* 100: 1407–1421.
- WOO, M., and A. OHMURA. 1997. The Arctic Islands. In W. R. Rouse, W. G. Bailey, and T. R. Oke [eds.], *The surface climates of Canada*, 172–196. McGill-Queen's University Press, Montreal, QC, Canada.
- WOODLEY, E.J., and J. SVOBODA. 1994. Effects of habitat on variation of phenology and nutrient concentration among four common plant species of the Alexandria Fiord lowland. In J. Svoboda, and B. Freedman [eds.], *Ecology of a polar oasis: Alexandria Fiord, Ellesmere Island, Canada*, 157–175. North York, ON.
- WOOKEY, P.A., A.N. PARSONS, J.M. WELKER, J.A. POTTER, T. V. CALLAGHAN, J.A. LEE, and M.C. PRESS. 1993. Comparative responses of phenology and reproductive

development to simulated environmental change in sub-Arctic and High Arctic plants. *Oikos* 67: 490–502.

WOOKEY, P.A., C.H. ROBINSON, A.N. PARSONS, J.M. WELKER, M.C. PRESS, T. V. CALLAGHAN, and J.A. LEE. 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.

Appendices

A.1 Chapter 2 Supplementary Tables and Figures

Table A1.1 Mean start, peak and finish of flowering day of year (DOY) and duration of flowering in 2013 of species populations across sub-locales (Iqaluit: 1=Apex, 2=Iqaluit city, 3=Sylvia Grinnell Territorial Park, 4=Road to Nowhere; Lake Hazen: 5=Camp Hazen, 6=Skeleton Lake, 7=plateau below and south east of McGill Mountain and 8=north east upper slopes of McGill Mountain) at Lake Hazen, Quttinirpaaq National Park, Ellesmere Island, Nunavut and Iqaluit, Baffin Island, Nunavut. Reprinted with permission from The University of Chicago Press.

Species	Location	Sub-locale	Start flower DOY	Peak flower DOY	Finish flower DOY	Flower duration
<i>Arnica angustifolia</i>	Hazen	7	-	212	-	-
	Iqaluit	1, 2	-	205	-	-
<i>Bistorta vivipara</i>	Hazen	5, 6	202	208	-	-
	Iqaluit	1, 2	199	212	-	-
<i>Cardamine bellidifolia</i>	Hazen	8	200	203	209	10
	Iqaluit	1, 3	190	193	202	12
<i>Cassiope tetragona</i>	Hazen	5, 8	184	193	211	27
	Iqaluit	1, 2, 3	178	189	206	28
<i>Cerastium arcticum</i>	Hazen	8	203	207	-	-
	Iqaluit	1, 2, 3	180	203	-	-
<i>Chamerion latifolium</i>	Hazen	5	201	203	211	10
	Iqaluit	1, 2, 3	201	215	228	27
<i>Draba corymbosa</i>	Hazen	6	187	194	199	12
	Iqaluit	1, 2, 3	181	189	198	17
<i>Draba nivalis</i>	Hazen	5	176	182	188	12
	Iqaluit	1	192	199	210	18
<i>Dryas integrifolia</i>	Hazen	5	179	186	203	24
	Iqaluit	1, 2, 3	173	186	209	36
<i>Eutrema edwardsii</i>	Hazen	6	187	191	201	14
	Iqaluit	1	186	196	206	20
<i>Oxyria digyna</i>	Hazen	5	187	190	198	12
	Iqaluit	2	163	172	180	17
<i>Pedicularis hirsuta</i>	Hazen	5	184	189	198	14
	Iqaluit	1, 2, 3	181	187	204	22
<i>Potentilla hyparctica</i>	Hazen	5, 8	197	202	207	11
	Iqaluit	1, 3	169	177	188	19
<i>Ranunculus hyperboreus</i>	Hazen	7	204	-	-	-
	Iqaluit	2	205	-	-	-
<i>Saxifraga cernua</i>	Hazen	8	206	206	-	-
	Iqaluit	2, 3	207	205	-	-
<i>Saxifraga cespitosa</i>	Hazen	8	189	-	-	-
	Iqaluit	1, 2	184	-	-	-
<i>Saxifraga nivalis</i>	Hazen	8	200	207	-	-
	Iqaluit	1	175	186	-	-
<i>Saxifraga oppositifolia</i>	Hazen	5, 8	166	176	191	26
	Iqaluit	1, 2, 3	161	164	173	13
<i>Saxifraga tricuspidata</i>	Hazen	5, 6, 8	194	206	-	-
	Iqaluit	2, 3	185	208	-	-
<i>Silene acaulis</i>	Hazen	7	194	202	-	-
	Iqaluit	1, 2	179	194	-	-
<i>Silene involucreta</i>	Hazen	5	182	191	203	22
	Iqaluit	1, 2, 3	172	188	206	34
<i>Silene uralensis</i>	Hazen	6, 7	200	203	207	7
	Iqaluit	2	192	203	210	18
<i>Stellaria longipes</i>	Hazen	5, 6	179	203	-	-
	Iqaluit	1, 2	183	207	-	-

Table A1.2 Mean start, peak, finish of flowering day of year (DOY) and duration of flowering in 2014 of N tagged plants across sub-locals (Iqaluit: 1=Apex, 2=Iqaluit city, 3=Sylvia Grinnell Territorial Park, 4=Road to Nowhere; Lake Hazen: 5=Camp Hazen, 6=Skeleton Lake, 7=plateau south east of McGill Mountain and 8=north east upper slopes of McGill Mountain) at Lake Hazen, Quttinirpaq National Park, Ellesmere Island, Nunavut and Iqaluit, Baffin Island, Nunavut. Reprinted with permission from The University of Chicago Press.

Species	Location	Sub-locale	Start flower DOY			Peak flower DOY			Finish flower DOY			Duration of flowering		
			Mean	N	Std Dev	Mean	N	Std Dev	Mean	N	Std Dev	Mean	N	Std Dev
<i>Alopecurus magellanicus</i>	Hazen	6, 7	185.8	56	2.26	186	56	2.26	193	56	2.54	7	56	2.67
	Iqaluit	3	188.5	30	2.83	189	30	2.83	197	30	2.63	9	30	2.86
<i>Arctagrostis latifolia</i>	Hazen	6	200.2	19	2.97	200	19	2.97	208	19	1.26	8	19	3.05
	Iqaluit	1, 3	208.2	59	4.39	208	59	4.39	217	59	2.56	9	59	3.43
<i>Arnica angustifolia</i>	Hazen	7	190.3	19	2.00	194	19	2.56	197	19	3.35	7	19	2.27
	Iqaluit	1, 3	187.7	56	6.17	193	56	5.24	200	56	4.99	12	56	4.39
<i>Bistorta vivipara</i>	Hazen	6	198.4	33	5.56	201	33	5.36	-	-	-	-	-	-
	Iqaluit	1, 4	199.5	30	4.24	206	30	4.87	-	-	-	-	-	-
<i>Cardamine bellidifolia</i>	Hazen	8	185.2	12	4.59	190	12	5.43	199	12	7.24	14	12	7.29
	Iqaluit	1, 3	190.7	26	10.96	198	26	13.33	210	26	13.46	20	26	13.21
<i>Cassiope tetragona</i>	Hazen	5, 7	180.5	49	5.81	187	49	6.19	201	41	5.10	21	41	8.54
	Iqaluit	1, 3	175.8	30	5.30	182	30	4.41	197	30	4.52	21	30	6.19
<i>Cerastium arcticum</i>	Hazen	8	184	22	4.70	191	22	6.56	205	22	6.89	21	22	7.48
	Iqaluit	1, 4	189.8	54	6.48	198	54	4.55	209	54	6.35	19	54	9.90
<i>Chamerion latifolium</i>	Hazen	5	192.9	19	3.77	194	19	3.42	199	19	4.58	6	19	3.34
	Iqaluit	1, 4	204.4	58	5.10	212	58	4.25	225	58	4.07	20	58	5.31
<i>Dryas integrifolia</i>	Hazen	5	175.2	21	2.90	177	21	1.30	183	21	2.87	8	21	3.66
	Iqaluit	1, 4	181.2	58	7.49	188	58	5.55	201	58	4.33	19	58	9.08
<i>Eriophorum scheuchzeri</i>	Hazen	6	186	30	2.03	186	30	2.03	191	30	2.85	5	30	1.96
	Iqaluit	1, 4	182	60	1.01	184	60	0.50	203	60	5.45	21	60	5.20
<i>Eutrema edwardsii</i>	Hazen	6	179.5	41	3.89	182	41	3.33	188	41	3.46	8	41	3.14
	Iqaluit	2, 4	170.6	59	4.14	174	59	3.98	182	59	3.58	11	59	3.81
<i>Pedicularis hirsuta</i>	Hazen	5	175.8	16	4.20	177	16	3.86	181	16	3.96	6	16	2.39
	Iqaluit	1, 3	179.3	58	4.22	182	58	4.25	192	58	4.66	12	58	4.05
<i>Saxifraga cespitosa</i>	Hazen	8	191.4	29	10.21	198	29	10.51	-	-	-	-	-	-
	Iqaluit	1, 2, 3	192	38	8.95	196	38	8.79	-	-	-	-	-	-
<i>Saxifraga oppositifolia</i>	Hazen	5, 8	166.1	60	6.43	171	60	7.22	180	60	9.60	14	60	5.05
	Iqaluit	2, 3	162.4	38	5.75	166	38	5.60	175	38	4.16	12	38	4.65
<i>Saxifraga tricuspidata</i>	Hazen	6, 7, 8	188	73	5.42	197	73	6.56	-	-	-	-	-	-
	Iqaluit	1, 3	191.6	53	5.86	203	53	5.72	-	-	-	-	-	-
<i>Silene acaulis</i>	Hazen	7	181.8	30	2.36	186	30	1.86	201	30	7.57	19	30	8.68
	Iqaluit	1, 2, 4	184.2	59	7.01	191	59	6.54	204	59	8.22	20	60	7.84
<i>Silene uralensis</i>	Hazen	6	183.6	29	2.92	187	29	3.10	194	29	4.55	11	29	4.39
	Iqaluit	1, 2, 3	197.3	56	7.03	199	56	7.09	205	56	7.48	8	56	4.46
All species	Hazen	5 - 8	184	558	9.84	188	558	10.12	194	469	10.05	12	415	7.64
	Iqaluit	1 - 4	188	822	12.86	193	822	13.12	204	822	14.05	15	702	7.93

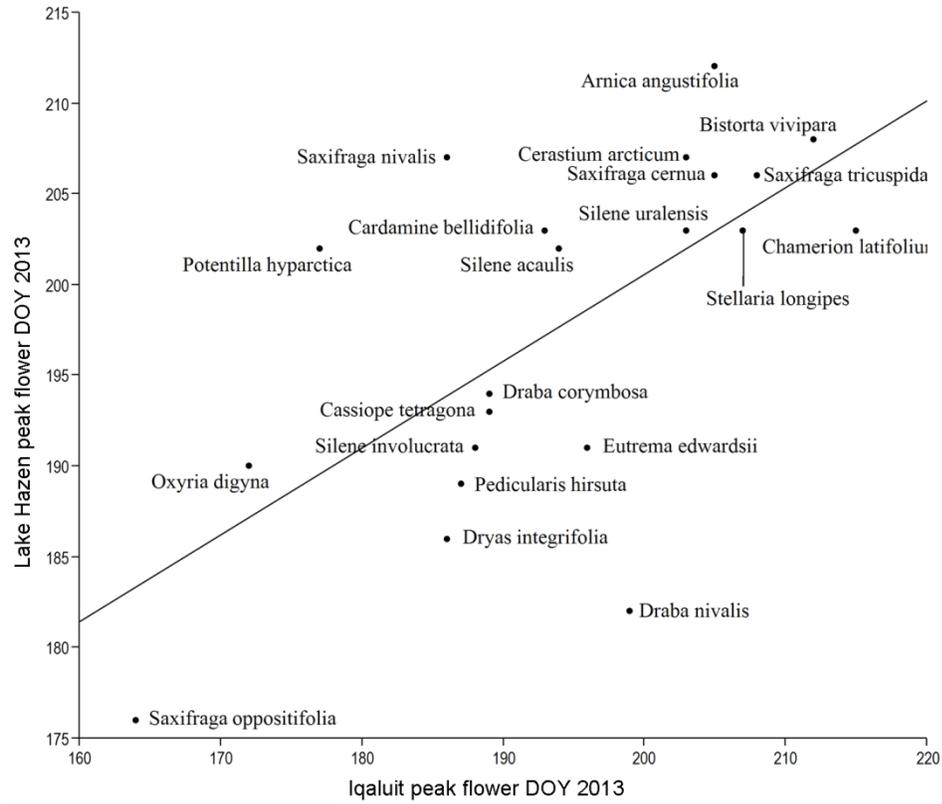


Figure A1.1 Comparison of order of peak flowering by species in 2013 at Lake Hazen, Ellesmere Island, Nunavut and Iqaluit, Baffin Island, Nunavut showing that the order of peak flowering is consistent between Iqaluit and Lake Hazen ($R^2 = 0.42$, $\rho = 0.64$, $P < 0.002$, $N = 21$). Reprinted with permission from The University of Chicago Press.

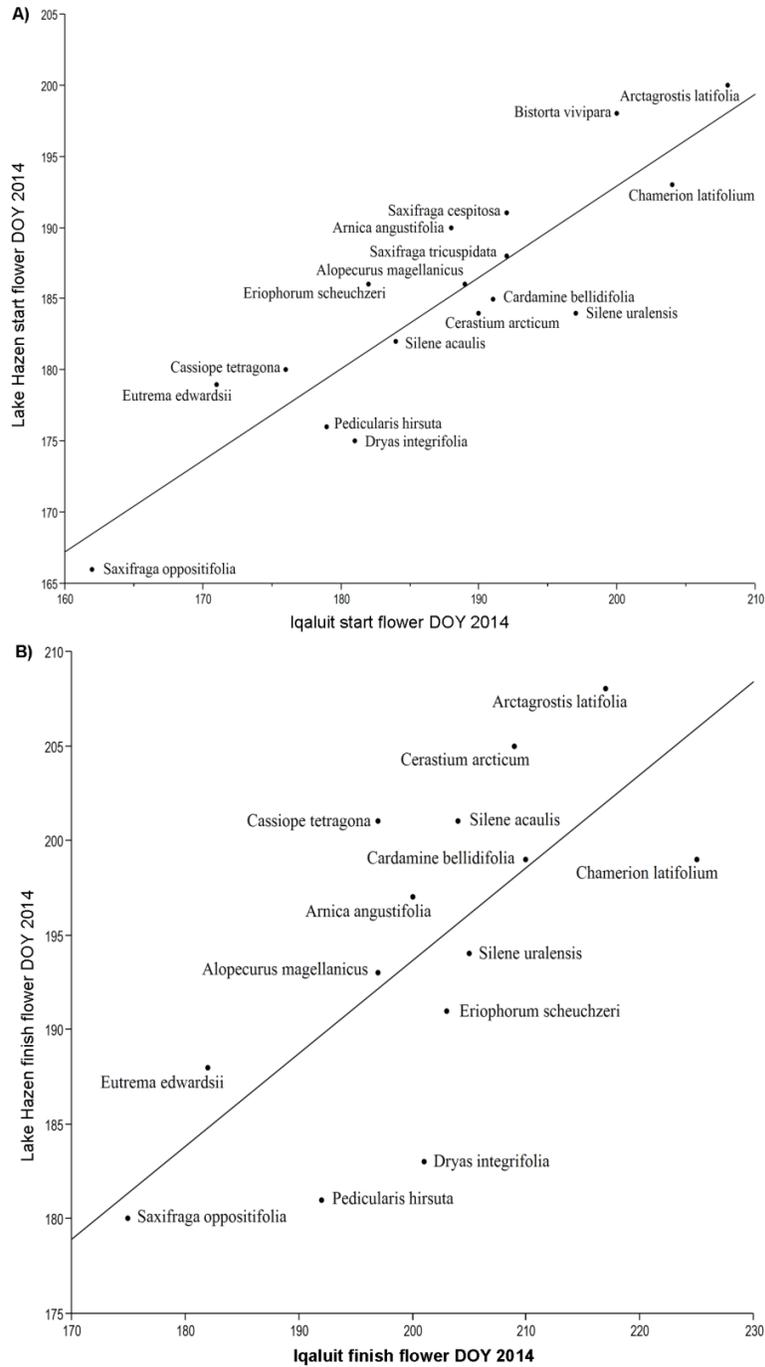


Figure A1.2 Comparison of order start flowering (A) and finish flowering (B) by species in 2014 at Lake Hazen, Ellesmere Island, Nunavut and Iqaluit, Baffin Island, Nunavut showing that the order of start and finish flowering is consistent between Iqaluit and Lake Hazen (start of flowering: $R^2 = 0.80$, $\rho = 0.85$, $P < 0.0001$, $N = 17$; finish of flowering: $R^2 = 0.52$, $\rho = 0.71$, $P < 0.005$, $N = 14$).

Reprinted with permission from The University of Chicago Press.

A.2 Chapter 4 Supplementary Tables

Table A2.1. Tanquary Fiord, Quttinirpaaq National Park, Nunavut, Canada monthly temperature reconstruction formulas and the correlation of 1989-2014 Tanquary Fiord monthly temperatures and 1989-2014 Eureka Environment Canada Weather Station, Nunavut, Canada monthly temperatures.

Reprinted with permission from Canadian Science Publishing.

	Eureka to Tanquary Fiord conversion formula	R^2	N	P
January Average Max. Temp.	$5.9169199 + 1.1184415 * \text{Eureka January Mean Max. Temp.}$	0.74	21	<0.0001
January Average Mean Temp.	$10.829435 + 1.2334527 * \text{Eureka January Mean Temp.}$	0.81	21	<0.0001
January Average Min. Temp.	$14.680344 + 1.2959426 * \text{Eureka January Mean Min. Temp.}$	0.80	21	<0.0001
February Average Max. Temp.	$10.163494 + 1.2545122 * \text{Eureka February Mean Max. Temp.}$	0.77	20	<0.0001
February Average Mean Temp.	$13.15102 + 1.3028522 * \text{Eureka February Mean Temp.}$	0.79	20	<0.0001
February Average Min. Temp.	$18.435236 + 1.3897081 * \text{Eureka February Mean Min. Temp.}$	0.81	20	<0.0001
March Average Max. Temp.	$19.411559 + 1.529719 * \text{Eureka March Mean Max. Temp.}$	0.82	17	<0.0001
March Average Mean Temp.	$22.553867 + 1.5711064 * \text{Eureka March Mean Temp.}$	0.83	17	<0.0001
March Average Min. Temp.	$23.304084 + 1.5369215 * \text{Eureka March Mean Min. Temp.}$	0.77	17	<0.0001
April Average Max. Temp.	$1.2992085 + 0.9438226 * \text{Eureka April Mean Max. Temp.}$	0.59	20	<0.0001
April Average Mean Temp.	$0.2680027 + 0.9251027 * \text{Eureka April Mean Temp.}$	0.59	20	<0.0001
April Average Min. Temp.	$-1.357164 + 0.9000174 * \text{Eureka April Mean Min. Temp.}$	0.54	20	<0.0001
May Average Max. Temp.	$2.5589833 + 1.015468 * \text{Eureka May Mean Max. Temp.}$	0.79	21	<0.0001
May Average Mean Temp.	$2.1849294 + 0.9304663 * \text{Eureka May Mean Temp.}$	0.80	20	<0.0001
May Average Min. Temp.	$0.7746785 + 0.8009466 * \text{Eureka May Mean Min. Temp.}$	0.51	21	0.0003
June Average Max. Temp.	$1.3593256 + 0.9933547 * \text{Eureka June Mean Max. Temp.}$	0.79	18	<0.0001
June Average Mean Temp.	$0.7367499 + 1.2576216 * \text{Eureka June Mean Temp.}$	0.85	18	<0.0001
June Average Min. Temp.	$1.6897991 + 1.5158103 * \text{Eureka June Mean Min. Temp.}$	0.77	18	<0.0001
July Average Max. Temp.	$1.6235115 + 0.9256464 * \text{Eureka July Mean Max. Temp.}$	0.75	18	<0.0001
July Average Mean Temp.	$-3.163988 + 1.7345863 * \text{Eureka July Mean Temp.}$	0.86	18	<0.0001
July Average Min. Temp.	$-0.888874 + 2.0755209 * \text{Eureka July Mean Min. Temp.}$	0.80	18	<0.0001
August Average Max. Temp.	$2.2557674 + 0.9026323 * \text{Eureka August Mean Max. Temp.}$	0.83	20	<0.0001
August Average Mean Temp.	$1.870486 + 1.0332776 * \text{Eureka August Mean Temp.}$	0.86	20	<0.0001
August Average Min. Temp.	$2.1674821 + 1.1077926 * \text{Eureka August Mean Min. Temp.}$	0.85	20	<0.0001
Sept. Average Max. Temp.	$0.0940744 + 0.7460242 * \text{Eureka Sept. Mean Max. Temp.}$	0.75	20	<0.0001
Sept. Average Mean Temp.	$-0.087929 + 0.713549 * \text{Eureka Sept. Mean Temp.}$	0.73	20	<0.0001
Sept. Average Min. Temp.	$-0.744408 + 0.6788342 * \text{Eureka Sept. Mean Min. Temp.}$	0.65	20	<0.0001
October Average Max. Temp.	$-2.395282 + 0.7494511 * \text{Eureka October Mean Max. Temp.}$	0.55	20	0.0002
October Average Mean Temp.	$-0.786827 + 0.8229231 * \text{Eureka October Mean Temp.}$	0.51	20	0.0004
October Average Min. Temp.	$1.1789312 + 0.9018629 * \text{Eureka October Mean Min. Temp.}$	0.49	20	0.0006
Nov. Average Max. Temp.	$-4.420148 + 0.7245754 * \text{Eureka Nov. Mean Max. Temp.}$	0.58	20	0.0001
Nov. Average Mean Temp.	$-4.042734 + 0.7704184 * \text{Eureka Nov. Mean Temp.}$	0.62	20	<0.0001
Nov. Average Min. Temp.	$-5.331758 + 0.74788 * \text{Eureka Nov. Mean Min. Temp.}$	0.59	20	<0.0001
Dec. Average Max. Temp.	$4.6904105 + 1.0760756 * \text{Eureka Dec. Mean Max. Temp.}$	0.77	19	<0.0001
Dec. Average Mean Temp.	$7.8204339 + 1.150231 * \text{Eureka Dec. Mean Temp.}$	0.82	19	<0.0001
Dec. Average Min. Temp.	$1.7951711 + 1.0644991 * \text{Eureka Dec. Mean Temp.}$	0.81	19	<0.0001

Table A2.2. Tanquary Fiord, Quttinirpaaq National Park, Nunavut, Canada 1989-2014 mean, standard deviation, minimum, maximum and range of annual and monthly mean minimum, monthly mean maximum and monthly mean temperatures. Reprinted with permission from Canadian Science Publishing.

	Mean	Std Dev	N	Min	Max	Range
Annual Average Max. Temp.	-13.19	1.22	25	-15.65	-9.96	5.69
Annual Average Mean Temp.	-16.18	1.39	25	-18.67	-12.52	6.15
Annual Average Min. Temp.	-19.10	1.51	25	-21.66	-15.22	6.44
January Average Max. Temp.	-30.89	4.31	26	-38.71	-21.96	16.75
January Average Mean Temp.	-34.19	4.10	26	-41.59	-26.25	15.34
January Average Min. Temp.	-37.20	3.90	26	-43.77	-29.90	13.87
February Average Max. Temp.	-31.81	4.15	26	-38.76	-22.67	16.09
February Average Mean Temp.	-35.30	3.77	26	-41.56	-26.58	14.98
February Average Min. Temp.	-38.37	3.49	26	-44.08	-29.63	14.44
March Average Max. Temp.	-30.33	4.22	26	-36.28	-21.63	14.65
March Average Mean Temp.	-34.19	4.06	26	-39.42	-25.67	13.75
March Average Min. Temp.	-37.67	3.89	26	-43.49	-29.58	13.91
April Average Max. Temp.	-19.27	3.46	26	-26.03	-10.03	16.00
April Average Mean Temp.	-23.61	3.41	26	-30.42	-15.38	15.04
April Average Min. Temp.	-28.18	3.49	26	-35.86	-20.63	15.23
May Average Max. Temp.	-4.28	2.43	26	-10.01	0.26	10.27
May Average Mean Temp.	-7.01	2.22	26	-12.06	-2.75	9.30
May Average Min. Temp.	-9.64	2.37	26	-14.29	-4.98	9.31
June Average Max. Temp.	7.13	2.05	26	3.94	10.91	6.97
June Average Mean Temp.	4.72	1.99	26	1.36	7.93	6.57
June Average Min. Temp.	2.42	1.84	26	-0.89	5.48	6.37
July Average Max. Temp.	10.59	2.01	26	7.73	15.33	7.60
July Average Mean Temp.	7.82	2.33	26	3.95	13.02	9.07
July Average Min. Temp.	5.52	2.13	26	2.22	10.93	8.70
August Average Max. Temp.	7.33	1.96	26	3.68	10.18	6.50
August Average Mean Temp.	5.33	1.97	26	1.69	8.35	6.66
August Average Min. Temp.	3.30	1.91	26	-0.36	6.38	6.75
Sept. Average Max. Temp.	-2.55	1.66	26	-5.35	1.36	6.71
Sept. Average Mean Temp.	-4.39	1.83	26	-8.00	-1.04	6.95
Sept. Average Min. Temp.	-6.50	2.05	26	-11.31	-3.47	7.84
October Average Max. Temp.	-14.81	2.68	25	-20.01	-8.87	11.14
October Average Mean Temp.	-17.38	3.00	25	-23.26	-10.73	12.53
October Average Min. Temp.	-20.19	3.35	25	-26.55	-12.61	13.94
November Average Max. Temp.	-22.45	3.11	25	-29.43	-16.33	13.10
November Average Mean Temp.	-25.98	3.06	25	-32.23	-20.64	11.59
November Average Min. Temp.	-29.28	2.96	25	-35.19	-23.48	11.71
December Average Max. Temp.	-27.17	4.60	25	-37.60	-20.30	17.30
December Average Mean Temp.	-30.35	4.33	25	-39.80	-23.04	16.76
December Average Min. Temp.	-34.36	4.09	25	-44.40	-26.28	18.12

A.3 Chapter 5 Supplementary Tables

Table A3.1. Sources of flowering time and seed dispersal time data. The physical herbarium specimens were examined at CAN, DAO, TRTE and Tanquary Fiord herbaria and digitised specimens were examined from ACAD, QFA and ALA.

Collection source	Collection type	Collection Yrs	N
Canadian Museum of Nature, National Herbarium of Canada (CAN)	Herbarium	1896-2015	2073
Agriculture and Agri-Food Canada National Collection of Vascular Plants, Vascular Plant Herbarium (DAO)	Herbarium	1947-2005	939
University of Toronto at Mississauga Herbarium (TRTE)	Herbarium	1950-1991	231
Acadia University, E.C. Smith Herbarium (ACAD)	Herbarium	1927-1980	57
Université Laval, Herbier Louis-Marie (QFA)	Herbarium	1957-1993	53
University of Alaska, Fairbanks, Museum of the North (ALA)	Herbarium	1930-1999	50
Tanquary Fiord Herbarium	Herbarium	1988	11
Jason Carpenter personal collection	Photograph	2002-2012	93
Canadian Museum of Nature photograph portfolio	Photograph	1995-2015	20
Jennifer Doubt personal collection	Photograph	2004-2012	6
Zoe Panchen research work	Field observations	2013-2015	262

Table A3.2. Linear regressions for each species at each spatial scale with flowering DOY as the response variable and June mean temperature as the explanatory variable where temperature-sensitivity is β in days/ $^{\circ}$ C and grey shading indicates significant earlier flowering with warmer June mean temperature ($P < 0.05$) (dark grey = $R^2 \geq 0.1$ and pale grey, a weak trend = $R^2 < 0.1$).

Species	Nunavut				Nunavut Mainland				Nunavut Archipelago			
	R^2	N	P	β	R^2	N	P	β	R^2	N	P	β
<i>Androsace septentrionalis</i>	0.01	34	0.6817	0.54					0.01	26	0.6377	-0.76
<i>Arnica angustifolia</i>	0.12	115	0.0002	-2.30	0.26	33	0.0023	-2.11	0.09	82	0.0053	-2.50
<i>Chamerion latifolium</i>	0.00	171	0.4046	-0.32	0.06	47	0.0993	-0.92	0.00	124	0.6060	-0.26
<i>Diapensia lapponica</i>	0.08	54	0.0360	-2.05	0.00	18	0.8610	0.25	0.25	36	0.0020	-3.96
<i>Dryas integrifolia</i>	0.07	256	0.0000	-1.54	0.02	50	0.3571	-0.87	0.13	206	0.0000	-2.08
<i>Erigeron compositus</i>	0.06	48	0.0990	-1.81					0.06	48	0.0990	-1.81
<i>Erysimum pallasii</i>	0.16	57	0.0018	-2.29					0.16	54	0.0028	-2.26
<i>Eutrema edwardsii</i>	0.21	114	0.0000	-2.49	0.00	20	0.9830	0.03	0.31	94	0.0000	-3.28
<i>Pedicularis arctica</i>	0.32	109	0.0000	-3.96	0.61	10	0.0078	-3.81	0.28	99	0.0000	-3.95
<i>Pedicularis capitata</i>	0.14	119	0.0000	-2.20	0.46	15	0.0058	-2.64	0.11	104	0.0007	-2.13
<i>Pedicularis flammea</i>	0.07	62	0.0403	-1.87	0.01	19	0.6820	0.73	0.11	43	0.0319	-2.23
<i>Pedicularis hirsuta</i>	0.10	191	0.0000	-1.90	0.03	20	0.4346	-0.68	0.12	171	0.0000	-2.22
<i>Pedicularis lapponica</i>	0.18	70	0.0002	-2.82	0.15	40	0.0120	-2.01	0.48	30	0.0000	-8.11
<i>Ranunculus nivalis</i>	0.13	93	0.0005	-2.84					0.18	90	0.0000	-3.46
<i>Ranunculus sulphureus</i>	0.05	148	0.0043	-1.63					0.05	147	0.0052	-1.62
<i>Saxifraga aizoides</i>	0.08	60	0.0310	-1.51	0.16	16	0.1199	-2.23	0.16	44	0.0073	-2.65
<i>Saxifraga cernua</i>	0.05	225	0.0005	-1.41	0.10	48	0.0267	-1.70	0.07	177	0.0004	-1.79
<i>Saxifraga cespitosa</i>	0.05	290	0.0002	-1.37	0.03	37	0.3301	-0.83	0.06	253	0.0002	-1.66
<i>Saxifraga flagellaris</i>	0.09	127	0.0008	-2.06					0.09	127	0.0008	-2.06
<i>Saxifraga hirculus</i>	0.05	165	0.0060	-1.43	0.01	35	0.6768	-0.39	0.07	130	0.0032	-2.13
<i>Saxifraga oppositifolia</i>	0.12	260	0.0000	-2.26	0.01	27	0.6293	-0.52	0.16	233	0.0000	-2.75
<i>Saxifraga tricuspidata</i>	0.10	196	0.0000	-1.88	0.07	56	0.0433	-1.48	0.12	140	0.0000	-2.34
<i>Tofieldia pusilla</i>	0.24	58	0.0001	-2.23	0.34	23	0.0036	-1.86	0.28	35	0.0012	-3.58

Species	Baffin Island				Ellesmere Island				Iqaluit				Lake Hazen			
	<i>R</i> ²	N	<i>P</i>	β	<i>R</i> ²	N	<i>P</i>	β	<i>R</i> ²	N	<i>P</i>	β	<i>R</i> ²	N	<i>P</i>	β
<i>Androsace septentrionalis</i>					0.03	17	0.5183	1.08					0.01	10	0.7800	-0.52
<i>Arnica angustifolia</i>	0.16	38	0.0129	-3.8	0.04	32	0.2959	-1.69	0.50	16	0.0021	-7.8	0.17	14	0.1459	-2.87
<i>Chamerion latifolium</i>	0.00	58	0.7373	-0.3	0.00	42	0.9034	-0.08	0.03	30	0.3587	-1.6	0.05	19	0.3756	-1.21
<i>Diapensia lapponica</i>	0.23	35	0.0038	-3.5					0.48	22	0.0003	-9.6				
<i>Dryas integrifolia</i>	0.11	61	0.0090	-2.3	0.03	66	0.1622	-1.06	0.18	27	0.0293	-3.7	0.14	19	0.1207	-1.77
<i>Erigeron compositus</i>					0.00	31	0.9772	-0.03					0.03	18	0.4607	-0.75
<i>Erysimum pallasii</i>					0.22	37	0.0037	-2.08					0.33	20	0.0080	-2.47
<i>Eutrema edwardsii</i>	0.14	24	0.0681	-3.1	0.40	28	0.0003	-2.63	0.41	12	0.0239	-7.7	0.51	11	0.0130	-1.88
<i>Pedicularis arctica</i>					0.27	58	0.0001	-3.23					0.25	27	0.0076	-2.55
<i>Pedicularis capitata</i>					0.05	50	0.1286	-1.15					0.10	21	0.1547	-1.40
<i>Pedicularis flammea</i>	0.12	42	0.0254	-2.4					0.34	27	0.0014	-6				
<i>Pedicularis hirsuta</i>	0.09	75	0.0111	-1.9	0.05	56	0.0894	-1.37	0.32	34	0.0004	-6.2	0.06	21	0.2659	-1.39
<i>Pedicularis lapponica</i>	0.48	30	<0.0001	-8.1					0.63	22	<0.0001	-8.3				
<i>Ranunculus nivalis</i>	0.19	70	0.0001	-4.3					0.18	26	0.0312	-5.8				
<i>Ranunculus sulphureus</i>					0.00	67	0.6636	-0.38					0.30	23	0.0073	-2.76
<i>Saxifraga aizoides</i>	0.18	31	0.0179	-3					0.43	20	0.0018	-8.1				
<i>Saxifraga cernua</i>	0.08	55	0.0332	-2.1	0.01	40	0.4994	-0.79	0.34	20	0.0069	-5.4	0.22	11	0.1426	-3.51
<i>Saxifraga cespitosa</i>	0.05	60	0.0842	-1.8	0.02	66	0.2426	-1.02	0.50	21	0.0004	-6	0.11	21	0.1517	-1.96
<i>Saxifraga flagellaris</i>					0.04	49	0.1457	-1.32					0.16	17	0.1089	-2.58
<i>Saxifraga hirculus</i>	0.00	16	0.8509	0.63	0.08	36	0.1060	-2.11					0.45	12	0.0167	-3.47
<i>Saxifraga oppositifolia</i>	0.20	65	0.0002	-4.3	0.07	76	0.0218	-1.65	0.20	32	0.0104	-5.8	0.01	24	0.5706	-0.80
<i>Saxifraga tricuspis</i>	0.15	52	0.0042	-3	0.05	45	0.1521	-1.35	0.33	27	0.0017	-6.3	0.22	20	0.0384	-2.09
<i>Tofeldia pusilla</i>	0.36	30	0.0005	-4.2					0.33	15	0.0246	-4.1				

Table A3.3. Mean monthly temperature regime shift analysis for annual, June and July mean temperatures for the 11 long-term weather stations in Nunavut using a nonlinear least squares models where break pt. yr. is the estimated year of the regime shift and β is the rate of change in temperature before and after the regime shift. Blue shading indicates a significant cooling trend (negative β) and orange shading indicates a significant warming trend (positive β).

	Break Pt. Yr.	Pre Break Point				Post Break Point			
		R ²	P	N	β	R ²	P	N	β
Alert Annual Mean	1982	0.08	0.0854	37	-0.020	0.41	<0.0001	34	0.068
Alert June Mean	1975	0.18	0.0212	30	-0.055	0.11	0.0319	41	0.041
Alert July Mean	1976	0.05	0.2278	31	-0.034	0.04	0.2428	40	0.016
Baker Lake Annual Mean	1987	0.00	0.6746	42	0.005	0.25	0.0062	29	0.072
Baker Lake June Mean	1973	0.04	0.3255	28	0.047	0.00	0.7250	43	0.009
Baker Lake July Mean	none								
Cambridge Bay Annual Mean	1964	0.08	0.2507	19	-0.033	0.34	<0.0001	52	0.052
Cambridge Bay June Mean	1996	0.09	0.0292	51	0.046	0.00	0.8662	20	-0.010
Cambridge Bay July Mean	none								
Clyde Annual Mean	1990	0.13	0.0157	45	-0.027	0.27	0.0060	26	0.086
Clyde June Mean	none								
Clyde July Mean	1972	0.16	0.0360	27	-0.066	0.29	0.0002	44	0.056
Coral Harbour Annual Mean	1989	0.00	0.7175	44	-0.005	0.22	0.0137	27	0.084
Coral Harbour June Mean	none								
Coral Harbour July Mean	none								
Eureka Annual Mean	1975	0.23	0.0066	30	-0.048	0.42	<0.0001	41	0.073
Eureka June Mean	1974	0.17	0.0244	29	-0.079	0.18	0.0045	42	0.064
Eureka July Mean	1994	0.00	0.6294	49	0.005	0.19	0.0429	22	0.105
Hall Beach Annual Mean	1974	0.18	0.0202	29	-0.054	0.31	0.0001	42	0.061
Hall Beach June Mean	none								
Hall Beach July Mean	none								
Iqaluit Annual Mean	1989	0.07	0.0803	44	-0.026	0.23	0.0113	27	0.096
Iqaluit June Mean	none								
Iqaluit July Mean	none								
Isachsen Annual Mean	1974	0.12	0.0703	29	-0.034	0.42	<0.0001	42	0.066
Isachsen June Mean	1977	0.12	0.0643	29	-0.060	0.13	0.0215	42	0.049
Isachsen July Mean	2002	0.00	0.7118	57	-0.004	0.14	0.1825	14	0.217
Pond Inlet Annual Mean	1986	0.08	0.0759	41	-0.024	0.34	0.0007	30	0.081
Pond Inlet June Mean	1985	0.00	0.8903	40	-0.002	0.15	0.0312	31	0.055
Pond Inlet July Mean	1977	0.00	0.8467	32	-0.004	0.36	<0.0001	39	0.069
Resolute Annual Mean	1983	0.05	0.1923	38	-0.018	0.40	<0.0001	33	0.837
Resolute June Mean	1968	0.17	0.0478	23	-0.092	0.13	0.0123	48	0.049
Resolute July Mean	2002	0.00	0.9653	57	0.000	0.22	0.0899	14	0.229