Detection and Attribution of Long-Term Vegetation Changes in Northern Alaska

Robert Thomas-Slider Barrett

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ABSTRACT

Climate change is impacting terrestrial ecosystems world-wide and the Arctic is particularly vulnerable as it is warming faster and with greater magnitude than other regions. Understanding the responses of arctic plants species to abiotic factors is crucial to predicting the impact climate change will have on the Arctic because plants play critical roles in carbon exchange, energy balance, and trophic interactions. Using data from long-term research sites in Barrow and Atqasuk, Alaska, the purpose of this thesis was to investigate how arctic plants respond to 17-19 years of experimental warming, establish the relative strengths of various abiotic factors in predicting the response of plant traits over time, and examine evidence that climate change will significantly affect plants as the region continues to warm. Plants typically responded to long-term experimental warming with increased inflorescence heights, increased leaf lengths, and accelerated reproductive phenologies, while reproductive efforts responded less consistently. Further analysis revealed that responses to experimental warming tended to dampen during warmer years. Though mostly non-significant, several abiotic factors showed trends over time consistent with regional warming patterns observed in the Barrow area including increasing air and soil temperatures, earlier snowmelts, delayed freeze-ups, drier soils, and increasing thaw depths. Several plant species showed significant trends toward increasing inflorescence heights and reproductive efforts over the same time period. Of the abiotic factors examined, air and soil temperatures yielded the greatest predictive capabilities as these factors were consistently correlated with the greatest number of traits across sites. Unlike other traits, the reproductive efforts of many species were best predicted using temperatures during the year prior to flower burst. When we compared experimental warming responses with trends in abiotic factors and traits over time we found strong evidence that climate change will likely cause significant shifts

in the growth and reproductive efforts of at least seven plant species at these sites. This study illustrates the value of long-term monitoring coupled with experimentation and lays the groundwork for future studies examining the ecosystem consequences of climate change on the Barrow region.

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CHAPTER I: INTRODUCTION TO STUDY

CLIMATE CHANGE IMPACTS ON TERRESTRIAL ECOSYSTEMS

Global climate change has greatly impact ecosystems worldwide (IPCC, 2013). Several impacts of climate change have been observed in terrestrial ecosystems, including changes in plant developmental timing, growth, and range (Sherry et al. 2007; Penuelas et al. 2009; IPCC 2013). Arctic ecosystems are especially vulnerable to climate change as the Arctic is warming faster and with greater magnitude than other biomes (ACIA 2005; IPCC 2013). Over recent years, studies have shown increased temperatures, accelerated snowmelt, increased winter precipitation, permafrost degradation, and increased growing season length in several Arctic regions (ACIA 2004). These changes have been associated with north-ward expansion of shrubs and trees, changes in plant robustness & developmental timing, and altered community compositions (ACIA 2004).

It is anticipated that impacts of climate change in the Arctic will have global repercussions through positive feedback mechanisms. Warmer temperatures are expected to hasten decomposition rates, consequently releasing large amounts of CO2 and methane, in turn amplifying the greenhouse effect leading to further warming (Chapin et al. 2000; Aerts 2006). Warming is also likely to also reduce snow and ice cover leaving water, soil, and vegetation exposed. The corresponding reduction in albedo will likely accelerate warming and cause faster melting of snow and ice (Chapin et al. 2005). Because they play critical roles in both of these processes, understanding the effects of climate change on Arctic plants is critical to predicting how changing tundra will impact the globe.

Additionally, plant phenology, including leaf and flower burst, influences food quality for herbivores. For example, Post and Forchhammer (2008) found evidence that the accelerated development of plants in Greenland negatively impacted the reproductive fitness of a caribou herd. Along with changes in the phenology of individual species, shifts in plant community composition have been observed, including the north-ward expansion of shrubs and trees into areas previously dominated by forbs and graminoids (Tape et al. 2006). This process is generally associated with increased canopy height and complexity resulting in increased air temperatures (Chapin et al. 2005).

ARCTIC PLANTS

The Arctic is characterized by cold temperatures and consequently low levels of nutrient turnover and availability. Arctic plants utilize a variety of mechanisms to cope with these constraints. As temperatures are typically warmer near the ground than at canopy height, many plants maintain a low stature, keeping their growing and photosynthetic tissues warm, while simultaneously avoiding wind damage (Savile 1972). Additionally, many species grow in dense clusters, maintain dead tissues, and exhibit hairy stems and leaves (Savile 1972). Tundra plants also maintain high concentrations of fats and specialized sugars in their tissues that prevent them from freezing (Billings & Mooney 1968). Arctic plants are capable of growing at much lower temperatures than plants in warmer ecosystems (Bliss 1971). This is accomplished, in part, by maintaining high levels of enzymes in their tissues (Chapin & Shaver 1985a). Furthermore, it is believed that tundra plants have adapted to handle nutrient stress by being long-lived and keeping high levels of nutrients in their tissues (Billings & Mooney 1968; Chapin & Shaver 1985a). Many store large amounts of carbohydrates in their roots, leaves, stems and draw on these stores early in the growing season so as to maximize their opportunity to grow and reproduce (Billings & Mooney 1968).

Other adaptations to the direct and indirect constraints of cold temperatures can be seen in arctic plant reproductive strategies. For instance, to bypass the expensive process of sexual reproduction many species reproduce vegetatively (Savile 1972). Also, most flowering plants produce buds one or more seasons in advance, allowing them to cope with short cold growing seasons (Sørensen 1941). It is apparent that temperature greatly affects Arctic plants as it has shaped their form and function and plays a critical role in determining the initiation of growing season, timing of flowering, seed dormancy, metabolic and photosynthetic rates, and onset of senescence (Billings & Mooney 1968; Bliss 1971).

CLIMATE CHANGE IMPACTS ON ARCTIC PLANTS: OBSERVATIONS AND EXPERIMENTS

Because low temperatures and nutrient availability constrain the morphology and physiology of arctic plants, it is widely believed that climate change will dramatically affect arctic species, in turn altering community interactions and ultimately community composition. In general, studies have shown that the impacts of warming on plants to vary greatly between species, location, and year (Hollister et al. 2005; Dunne et al. 2003). Effects of warming have primarily been assessed by examining responses to natural temperature variation and experimental warming (Thorhallsdottir 1998; Arft et al. 1999; Hollister et al. 2005a).

While studies of plant responses along natural temperature gradients are useful, they are unable to demonstrate causality. To address this, researchers have utilized artificial warming—comparing plant traits in experimental warming treatments with those in ambient conditions

(Arft et al. 1999; Shaver & Jonasson 1999; Marchand et al. 2004). Commonly, open-top fiberglass chambers (OTC's) are used to provide modest warming of 1-5˚C. Chambers have been used widely by researchers participating in a network of projects designed to forecast the responses of tundra vegetation to climate change, known as the International Tundra Experiment (ITEX). By following standardized protocols and establishing long-term research sites, ITEX has provided a great deal of information on the impacts of climate change on Arctic and Alpine plants (Arft et al. 1999; Walker et al. 2006).

Included as part of ITEX are four sites established in Northern Alaska established by Hollister and Webber in 1994-1996. Since their establishment, these sites have been used to examine the growth, developmental, and reproductive responses of Arctic plants to warming using OTC's (Hollister et al. 2005a). Hollister et al. (2005a) found plant responses to vary greatly between year, site, and species. Typically, species that responded significantly to several years of experimental warming did so with accelerated flowering, increased growth, and increased reproductive effort (Arft et al. 1999; Hollister et al. 2005a).

Warming manipulation has continued at the sites established by Hollister and Webber in 1994 and subsequently large amounts of data have been collected describing plant responses to experimental warming and ambient conditions throughout this time period. Because of this, an assessment of long-term responses to temperature is now possible. By examining the developmental, growth, and reproductive responses of Arctic plants to warming over time at these sites, this study investigated the long-term effects of warming on Arctic plants.

The objectives of this study (by chapter) were to:

1. Investigate abilities of plants to respond to experimental warming over a period of 17-19 years. This examination is detailed in Chapter II and is in press in the journal Polar Research (Barrett & Hollister in press).
2. Determine if abiotic factors have shifted at these study sites and if these changes have potentially led to significant responses among the study species. This examination is detailed in Chapter III and is published in the American Journal of Botany (Barrett et al. 2015).

Methods

STUDY SITES AND EXPERIMENTAL DESIGN

This study takes place at four sites in Northern Alaska: two in Barrow (71 18' N, 156 40' W) and two in Atqasuk (70 29' N, 157 25' W). Sites were established in dry heath and a wet meadow plant community types (Figs. 1 & 2). Dates of establishment are depicted in Fig. 1. At each site 48 $1m^2$ plots were established for vegetation monitoring. Of the 48 plots, 24 were randomly assigned to receive warming treatment while the other 24 were left as controls (Fig. 2). Warming was achieved using open-top chambers which increase ambient air temperatures ~2˚C. Chambers were placed on plots after snowmelt and removed in late august of each season. Additional plots of each treatment were established for collecting abiotic data at all sites.

Fig. 1 Photographs of study sites shown with years of establishment.

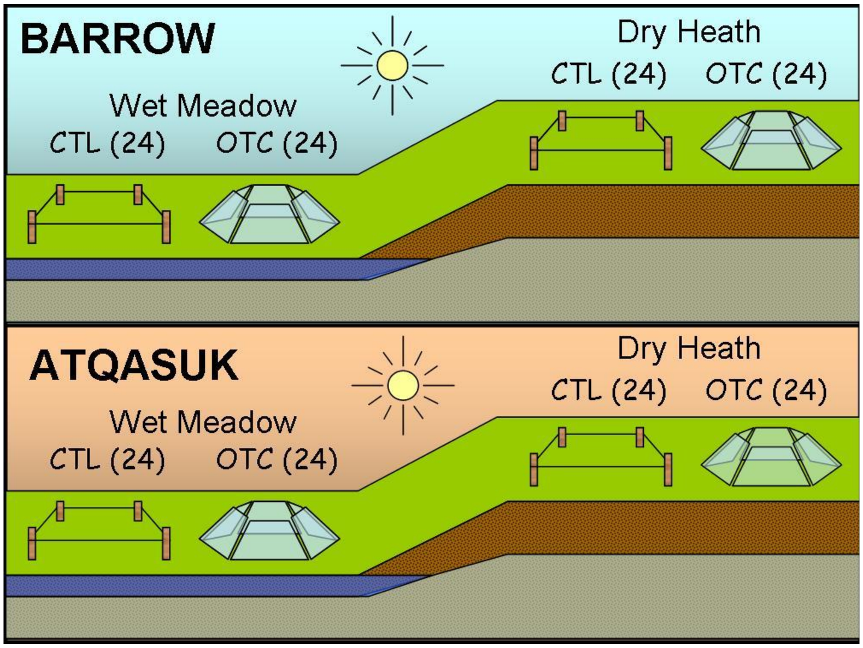


Fig. 2 Summary diagram depicting the experimental design. Sites of 24 control and 24 warmed plots OTC's were established along a temperature gradient (from cool Barrow to warmer Atqasuk) and a moisture gradient (from wet meadow to dry heath communities).

ABIOTIC MEASURES

At each site temperature, depth of soil thaw, light quantity, precipitation, and wind speed data were collected. These data were gathered using solar-powered meteorological stations at each site or manually in the case of soil thaw depth and each is discussed in further detail in the chapters that follow.

PLANT TRAIT MEASURES

Species present at each site are shown in Table 1. Growth, phenology, and reproductive effort were monitored for a large number of species at each site, but data were not collected for each species every year. Growth was observed by measuring leaf and inflorescence lengths. The phenological events recorded were date of leaf burst, bud appearance, inflorescence appearance, flower burst, flower wither, seed set, seed dispersal, and leaf senescence. Reproductive effort was monitored by counting the maximum number of inflorescences, buds, flowers, and fruits produced by a species.

During some years the growth, phenology, and reproductive effort of marked individuals of each species were tracked to provide better estimates of variability within plots. In several years the phenological progression of marked individuals of most species were recorded weekly, as were leaf and inflorescence lengths of marked graminoid individuals. In addition to tracking the progression of individuals, peak flowering times were examined by counting the total number of inflorescences in flower each week for several species.

Table 1 List of species present by study site. Bolded species are abundant enough to make reasonable generalizations.

Barrow Dry	Barrow Wet	Atqasuk Dry	Atqasuk Wet
Alopecurus alpinus	*Alopecurus alpinus*	*Antennaria friesiana*	*Betula nana*
Arctagrostis latifolia	*Arctophila fulva*	***Arctagrostis latifolia***	***Carex aquatilis***
Carex stans	***Calamagrostis holmii***	*Artemesia borealis*	***Carex rariflora***
Cassiope tetragona	***Cardamine pratensis***	***Carex bigelowii***	***Carex rotundata***
Draba lactea	***Carex stans***	***Cassiope tetragona***	***Dupontia psilosantha***
Draba micropetala	***Carex subspathacea***	***Diapensia lapponica***	***Eriophorum angustifolium***
Festuca brachyphylla	***Cerastium beeringianum***	***Hierachloe alpina***	***Eriophorum russeolum***
Juncus biglumis	*Chrysosplenium tetrandrum*	***Ledum palustre***	***Juncus biglumis***
Luzula arctica	*Cochlearia officinalis*	***Luzula arctica***	*Luzula wahlenbergii*
Luzula confusa	***Draba lactea***	***Luzula confusa***	***Pedicularis sudetica***
Oxyria digynia	*Draba micropetala*	*Minuartia obtusiloba*	*Polygonum viviparum*
Papaver hultenii	***Dupontia fisheri***	*Pedicularis lapponica*	***Salix polaris***
Papaver lapponicum	***Eriophorum russeolum***	***Polygonum bistorta***	***Salix pulchra***
Pedicularis kanei	*Eriophorum scheuchzeri*	***Salix phlebophylla***	*Saxifraga foliolosa*
Poa arctica	***Eriophorum triste***	***Trisetum spicatum***	
Poa malacantha	***Hierochloe pauciflora***	***Vaccinium vitis-idaea***	
Potentilla hyparctica	***Juncus biglumis***		
Ranunculus nivalis	***Luzula arctica***		
Ranunculus pygmaeus	***Luzula confusa***		
Salix rotundifolia	*Melandrium apetalum*		
Saxifraga caespitosa	*Pedicularis kanei*		
Saxifraga cernua	*Petasites frigidus*		
Saxifraga flagellaris	***Poa arctica***		
Saxifraga foliolosa	*Ranunculus nivalis*		
Saxifraga nivalis	*Ranunculus pygmaeus*		
Saxifraga punctata	*Salix pulchra*		
Senecio atropurpureus	*Salix rotundifolia*		
Stellaria laeta	*Saxifraga caespitosa*		
Vaccinium vitis-idaea	***Saxifraga cernua***		
	Saxifraga foliolosa		
	Saxifraga hieracifolia		
	Saxifraga hirculus		
	Stellaria humifusa		
	Stellaria laeta		

CHAPTER II: ARCTIC PLANTS ARE CAPABLE OF SUSTAINED RESPONSES TO LONG-TERM WARMING.

Introduction

In recent decades, climate change has been impacting terrestrial ecosystems world-wide (IPCC 2013). The responses of Arctic ecosystems have been of particular interest as the Arctic has been warming faster and with greater magnitude than other regions (ACIA 2005; IPCC 2013). The impact of climate change on the Arctic has been of particular interest owing to its importance regulating energy balance and the global carbon budget (Chapin et al. 2000; ACIA 2005; Aerts 2006). As tundra plants play crucial roles in these processes, understanding their response to warming is critical to predicting how the Arctic will respond to climate change. Experimental and observational studies have shown that arctic plants typically respond to warming with increased growth and reproduction and accelerated phenology (Chapin et al. 1995; Arft et al. 1999; Hollister et al. 2005a). Regional warming in the Arctic has also been associated with shrub expansion, shifts in plant community composition, altered trophic interactions, and changes in energy balance (Chapin et al. 2005; Post et al. 2008).

In assessing the impacts of climate change on plant species, one factor that remains unclear is how long the response of plants to warming can be maintained. Although ambient temperatures in the Arctic are typically lower than those optimal for photosynthesis in tundra species, it has been assumed that arctic ecotypes are poorly equipped to respond to long-term warming as a result of their metabolic and photosynthetic adaptations to life in cold climates (Billings & Mooney 1968; Bliss 1971; Chapin & Chapin 1981; Chapin & Shaver 1985a). This idea has been supported by transplant studies, which indicated that tundra species are likely to have difficulty surviving, growing, and reproducing in significantly warmer conditions (Chapin

& Chapin 1981; Shaver & Kummerow 1992; Bennington et al. 2012). Hence, a prevailing thought has been that, when subjected to warmer temperatures, arctic plants would exhibit short-term gains in growth and reproduction, followed by a diminished response as the plants exhausted their below-ground carbohydrate and nutrient stores (Shaver & Kummerow 1992; Chapin et al. 1995; Shaver & Jonasson 1999). Previous studies have seemingly supported this hypothesis as initial plant responses to warming decreased after a few years of exposure to experimental warming (Chapin & Chapin 1981; Arft et al. 1999). However, this line of thought is not supported by long-term field studies that have shown arctic plants continue to respond to warming after two decades of consistent exposure (Hudson & Henry 2009; Hudson et al. 2011; Elmendorf et al. 2012a). While more studies have focused on how long-term warming affects arctic plant community composition (Elmendorf et al. 2012b; Hedenås et al. 2012; Michelsen et al. 2012), less attention has been given to the how growth, reproduction, and phenological responses of individual species are affected by long-term warming (Hudson et al. 2011; Klady et al. 2011; Campioli et al. 2013).

In order to better understand how plant trait responses to warming change over time, we examined the responses of arctic plants to 17-19 years of experimental warming using four study sites that are part of the International Tundra Experiment (ITEX). Data from these sites have been used in previous analyses examining short-term community and species-level responses to warming (Hollister et al. 2005a, b; Oberbauer et al. 2007), and in more recent studies examining longer-term responses of tundra plants to temperature (Elmendorf et al. 2012; Oberbauer et al. 2013). By examining findings from these long-term research sites we sought to answer the following questions:

1. How did plants at these sites respond to long-term experimental warming and are responses comparable to those found in other studies?
2. How did responses to experimental warming vary over time and with respect to summer temperature?

Methods

STUDY SITES AND EXPERIMENTAL DESIGN

This study took place at field sites near Barrow and Atqasuk, Alaska. We collected data at two sites at each location—one in dry heath tundra and the other in wet meadow tundra. The Barrow Dry (BD) and Barrow Wet (BW) sites were established in 1994 and 1995, respectively while the Atqasuk Dry (AD) and Atqasuk Wet (AW) sites were established in 1996. For this analysis we used plant trait data from the following years: 1994-2001, 2007-2008, and 2010-2012. Each site included 48 permanently established plots of vegetation (~1 m^2), half of which were randomly assigned to be experimentally warmed using open-top chambers. For comprehensive details on these sites see Hollister (2003).

TEMPERATURE MEASURES

We collected temperatures at each site using sensors (Campbell Model 107 Temperature Probe or HOBO Temperature Logger or StowAway Temperature Logger) placed in radiation shields (gill six plates) at 10 to 15 cm above ground surface. Readings were taken every 10-60 minutes, then averaged and recorded every hour (CR10X Datalogger, Campbell Scientific, Logan, UT, USA; or HOBO or StowAway Temperature Logger, Onset Computer Corporation, Pocasset, MA, USA). As noted above we used a number of different sensors to measure canopy height temperature in a plot. In 1998 dataloggers were installed at the sites which measured screen and canopy height temperature as well as a host of other metrics. Prior to 1998, screen height temperatures were estimated from weather stations located within 3 km of the sites. Snowmelt dates were determined either through visual confirmation or, when researchers were not present for this event, using the day of year that the average soil surface temperatures remained above 0 °C at the site. Soil temperature at each site was measured with probes reported elsewhere (Hollister et al. 2006). In cases where temperature readings were not available due to instrument malfunction, readings from the paired site or the nearby weather station were substituted (Hollister et al. 2006). These cases were less than 5% of all readings. The resulting hourly temperature readings for the site were used to calculate thawing degree days from snowmelt (TDD) by summing average temperatures above 0 °C daily from first snow-free date until August 15.

PLANT TRAIT MEASURES

This study was designed to examine traits of many species over many years. Therefore, only a few plant traits were monitored annually based on the comparability across species and the ease of measuring consistently. Traits were chosen from those which others researchers agreed to collect using a common protocol for ITEX study sites (Molau 1993; Arft et al. 1999). The following traits were examined: inflorescence height, leaf length, reproductive effort, and reproductive phenology. Inflorescence height was measured as distance from ground to the tip of the inflorescence in forbs and graminoids and as the length from inflorescence base to tip in shrubs. Leaf lengths were measured as the length from the base of a plant to the tip of its longest leaf in graminoids and forbs, except *Potentilla hyparctica* and *Stellaria laeta* where leaf length was described as the distance from the base to the tip of the longest leaf. This same method was used for shrubs, except *Cassiope tetragona* where annual growth increments were used as leaf length. For both traits we used the average maximum size of an individual based on 1-6 individuals per plot, depending on abundance (we monitored up to three marked individuals per plot and to ensure that we recorded reproductive traits we measured the three largest flowering individuals per plot). We defined reproductive effort as either the number of flowers or number of inflorescences produced by a species in a given plot, depending on the morphology of the species. Similarly, reproductive phenology was defined as either the first day of year an inflorescence appeared or first day of year anthesis or stigma activation was observed in a plot. Plants were monitored for each trait multiple times per week in each plot, with the exception of plots during 2001 when only 10 plots of each treatment could be observed owing to logistical constraints. Detailed information on the plant trait measured for each species is provided in Hollister (2003).

STATISTICAL ANALYSES

We used simple linear regressions performed in R to investigate possible trends in ambient summer temperatures, represented as TDD, at each study site over time (R Development Core Team 2005).

Not all measurements were made each year on each plant species and only a few species were abundant across a site. Thus, analysis was constrained to species for which a given trait was measured in at least 5 plots per treatment during a given year and met this criterion for at least 5 years during the study period (see Appendix 1 in Barrett & Hollister in press for mean, standard deviation, and sample size of all plant traits included in the analysis organized by trait, site, species and year). Response to experimental warming was determined for each species and trait using effect sizes calculated as Hedges' d, which is the difference between the averages of the control ($\bar{X}^C$) and warmed ($\bar{X}^E$) traits for each species divided by their pooled SD (S) and multiplied by a term to correct for small sample size. This test statistic is found as:

$$d = \frac{(\bar{X}^E - \bar{X}^C)}{S} \times \left(1 - \frac{3}{4(n_e + n_c - 2) - 1}\right)$$

where n_e and n_c are the sample sizes of the control and warmed plants, respectively. This method treated each species, trait and year as an individual study. The studies were then also pooled by site and growth form within a site. Performing analyses this way allowed us to directly compare our findings to those of similar studies (Arft et al. 1999; Rosenberg et al. 2000; Dormann & Woodin 2002). We performed two additional analyses; one to assess whether effect sizes of experimental warming were changing over time, and another to discern if there was a relationship between effect sizes of experimental warming and summer temperature. Both analyses were performed using effect sizes calculated as Hedges' d as described above, but here the average plant trait values for each study site and year were treated as an individual study (thus the sample size for each point was the number of species that occurred at the site). We then used weighted least squares regressions to assess trends in effect sizes for each site over time and with respect to summer temperatures (TDD). Metawin v 2.1 was used for these analyses (Rosenberg et al. 2000). Effect sizes were considered significant when their 95% confidence interval did not overlap with an effect size of zero.

Results

TEMPERATURE PATTERNS

During the time of this study, temperatures in control plots showed non-significant warming tendencies over time at all four sites (Fig. 3; AD p = 0.50, AW p = 0.28, BD p = 0.31, BW p = 0.15). The chambers warmed the plots on average for the summer between 0.4 and 2.2 °C depending on the site and year (Table 2).

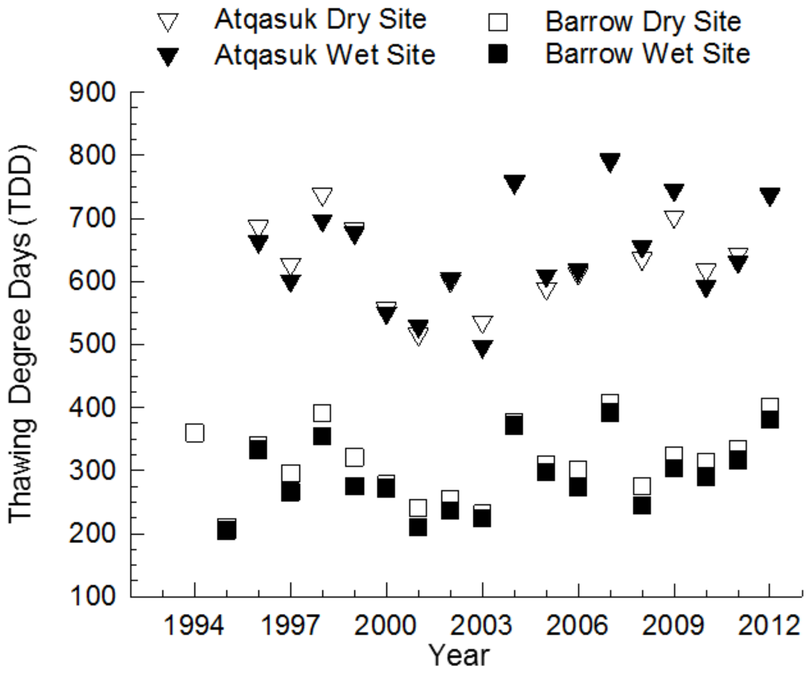


Fig. 3 Temperatures over time at the four study sites. Symbols represent average thawing degree days totals (TDD) for the summer at a given site in a given year. Lines represent results of linear regressions. The sample size was the number of years of the experiment (19 at Barrow Dry, 18 at Barrow Wet and 17 at both Atqasuk sites).

Table 2 Average snowmelt and daily summer temperature (°C) for years 1994-2012 at each study site. Temperatures were recorded at screen height (S, 2 m) and canopy height (10-15 cm) over control (C) and experimentally warmed (W) plots. Temperature differences between control and warmed plots at canopy height are also shown (W – C). Readings for screen height were made on one sensor only, canopy height readings were based on 1-12 plots that had sensors (when more than one plot was measured we calculated the average value to create one continuous record of hourly readings for the summer; from the one continuous reading we present the average value below).

Site	Dry Heath					Wet Meadow				
Year	Snowmelt	S	C	W	W-C	Snowmelt	S	C	W	W-C
Atqasuk										
1996	May 22	9.0	9.3	11.1	1.8	May 29	9.0	9.2	10.2	1.0
1997	Jun 09	8.4	9.9	11.6	1.7	Jun 16	8.4	10.0	10.9	0.9
1998	Jun 02	8.5	9.9	11.5	1.6	Jun 09	8.7	10.2	11.1	0.9
1999	Jun 09	9.3	10.0	11.6	1.6	Jun 10	9.3	10.0	11.1	1.1
2000	Jun 06	7.1	7.7	9.2	1.5	Jun 11	7.4	8.2	8.8	0.6
2001	Jun 04	6.4	7.1	8.1	1.0	Jun 10	7.2	7.6	8.4	0.8
2002	May 20	5.7	6.7	8.2	1.5	May 23	5.7	7.0	8.0	1.1
2003	June 05	6.3	7.4	8.3	0.9	June 07	6.3	7.1	8.4	1.3
2004	May 23	8.4	8.9	9.8	0.9	June 5	9.7	10.6	11.6	1.0
2005	June 08	7.4	7.8	8.9	1.1	June 12	7.7	8.5	9.0	0.5
2006	May 25	6.0	6.5	7.6	1.1	June 05	6.8	7.6	8.1	0.5
2007	June 02	9.4	10.1	11.5	1.5	June 03	9.4	10.3	11.2	0.9
2008	May 24	6.4	7.1	8.3	1.2	June 03	7.0	8.3	8.7	0.4
2009	May 20	7.1	7.7	8.8	1.1	May 26	7.4	8.6	9.0	0.4
2010	June 05	7.8	8.3	9.4	1.1	June 11	8.0	8.7	9.5	0.9
2011	May 22	7.1	7.3	8.3	1.0	May 30	7.6	7.8	8.5	0.6
2012	May 26	8.7	9.0	10.2	1.3	June 05	9.6	10.1	11.1	1.1
Average	May 30	7.6	8.3	9.6	1.3	June 05	8.0	8.8	9.6	0.8
Barrow										
1994	Jun 15	4.2	6.1	8.0	1.9	· .	· .	· .	· .	· .
1995	Jun 14	3.1	3.1	4.9	1.8	Jun 19	3.5	3.4	5.4	2.0
1996	May 30	3.7	4.3	6.1	1.8	Jun 10	3.8	4.8	6.2	1.4
1997	Jun 08	3.2	4.0	5.9	1.9	Jun 25	4.1	5.1	7.3	2.2
1998	Jun 03	3.9	5.2	6.9	1.7	Jun 20	4.8	6.3	7.8	1.5
1999	Jun 16	4.1	4.9	6.9	2.0	Jun 27	4.7	5.5	7.4	1.9

Table 2 contd.

Site	Dry Heath					Wet Meadow				
Year	Snowmelt	S	C	W	W-C	Snowmelt	S	C	W	W-C
2000	Jun 12	3.3	4.2	5.3	1.1	Jun 18	3.6	4.4	5.7	1.3
2001	Jun 12	2.5	3.2	4.7	1.5	Jun 21	2.7	3.5	5.4	1.9
2002	May 23	1.7	2.7	3.5	0.8	Jun 08	3.9	4.7	6.5	1.8
2003	June 08	2.6	3.3	4.8	1.5	June 23	3.2	4.1	5.5	1.3
2004	June 11	6.1	5.8	7.3	1.5	June 17	6.4	6.3	7.8	1.5
2005	June 10	4.0	4.1	5.5	1.4	June 24	4.7	4.8	6.9	2.1
2006	June 08	3.5	3.7	5.6	1.9	June 17	3.7	3.8	5.5	1.7
2007	June 07	5.7	5.9	8.0	2.1	June 15	6.1	6.3	8.8	2.5
2008	May 29	3.3	3.4	5.3	1.8	June 15	3.8	3.9	5.6	1.7
2009	May 29	4.1	4.1	5.4	1.3	June 14	4.7	4.8	6.2	1.4
2010	June 18	5.4	5.3	6.8	1.5	June 30	6.1	5.9	7.3	1.4
2011	May 27	4.1	4.1	5.5	1.4	June 18	5.2	5.2	7.0	1.8
2012	June 07	6.3	6.2	8.0	1.8	June 17	6.8	6.7	9.0	2.2
Average	June 07	3.9	4.4	6.0	1.6	June 18	4.5	5.0	6.7	1.8

PLANT TRAIT RESPONSES TO LONG-TERM EXPERIMENTAL WARMING

Species generally responded to experimental warming with increased inflorescence heights, earlier reproductive phenology, and increased leaf lengths, but responses of reproductive effort were not consistent (Table 3). When experimentally warmed, 79% percent of the species grew taller inflorescences and 51% grew longer leaves. Fewer species responded to experimental warming with a change in reproductive phenology (35%), but significant responders always flowered earlier when warmed. Even fewer species (29%) showed a significant response to experimental warming with respect to reproductive effort and roughly equal numbers of species had increased or decreased reproductive efforts when warmed.

VARIATION IN RESPONSE TO EXPERIMENTAL WARMING OVER TIME AND WITH SUMMER TEMPERATURE (THAWING DEGREE DAYS)

Plant responses to experimental warming were mostly consistent, with the exception of reproductive phenology which showed a significant (p = 0.03) trend toward decreasing effect sizes over time (Fig. 4D). However, we also note that inflorescence height, leaf length, and reproductive effort each showed non-significant tendencies toward reduced effect sizes over time (Fig. 4). For all four traits we found significant trends toward reduced response to experimental warming during warmer summers (Fig. 5).

Table 3 Effects of warming treatment on plant traits by site, growth form (GF), and species. The effect size from meta-analysis (Hedges' d) is reported when significant.

Site	GF	Species	Inflorescence height	Reproductive phenology	Leaf length	Reproductive effort
Atqasuk Dry Site						
	All	**All**	**0.33**	**-0.47**	**0.26**	**-0.18**
	Forb	**All**	**0.57**	**ns**	**ns**	**ns**
		Polygonum bistorta	0.57	ns	ns	ns
	Gram.	**All**	**0.34**	**ns**	**0.39**	**ns**
		Carex bigelowii	.	.	ns	.
		Hierachloë alpina	0.90	ns	0.48	ns
		Luzula arctica	ns	.	ns	ns
		Luzula confusa	ns	ns	0.33	ns
		Trisetum spicatum	.	.	0.74	.
	E. shrub	**All**	**ns**	**ns**	**0.14**	**-0.38**
		Cassiope tetragona	.	ns	ns	-0.43
		Diapensia lapponica	ns	ns	ns	-0.41
		Ledum palustre	.	ns	0.37	ns
		Vaccinium vitis-idaea	.	ns	ns	-0.70
Atqasuk Wet Site						
	All	**All**	**0.64**	**ns**	**0.46**	**ns**
	Gram.	**All**	**0.64**	**ns**	**0.48**	**ns**
		Carex aquatilis	0.58	ns	0.55	ns
		Dupontia psilosantha	.	.	0.49	.
		Eriophorum angustifolium	0.59	ns	0.50	ns
		Eriophorum russeolum	0.95	.	0.38	0.50
	Forb	**All**	**.**	**.**	**ns**	**.**
		Pedicularis sudetica	.	.	ns	.

Table 3 contd.

Site	GF	Species	Inflorescence height	Reproductive phenology	Leaf length	Reproductive effort
Barrow Dry Site						
	All	**All**	**1.13**	**-3.57**	**0.43**	**0.18**
	Forb	**All**	**1.14**	**-5.18**	**0.24**	**0.24**
		Papaver hultenii	0.87	-5.62	.	ns
		Pedicularis kanei	.	.	ns	.
		Potentilla hyparctica	1.65	-7.55	ns	ns
		Senecio atropurpureus	ns	ns	ns	.
		Stellaria laeta	.	-5.42	ns	0.67
		Saxifraga punctata	0.91	ns	0.58	ns
	Gram.	**All**	**1.13**	**-1.91**	**0.72**	**0.14**
		Arctagrostis latifolia	1.15	-3.21	0.61	ns
		Luzula arctica	1.00	ns	0.39	ns
		Luzula confusa	1.00	-2.39	0.95	ns
		Poa arctica	1.33	-2.32	0.81	0.37
	D. Shrub	**All**	**.**	**-1.71**	**0.26**	**-0.40**
		Salix rotundifolia ♀	.	ns	ns	-0.40
		Salix rotundifolia ♂	.	ns	ns	.
	E. Shrub	*Cassiope tetragona*	.	-6.30	ns	0.84
Barrow Wet Site						
	All	**All**	**0.92**	**-1.56**	**0.44**	**ns**
	Forb	**All**	**1.09**	**-1.51**	**0.21**	**ns**
		Cardamine pratensis	1.87	ns	0.48	0.53
		Cerastium beeringianum	.	.	ns	.
		Draba lactea	1.39	.	.	ns
		Saxifraga cernua	1.10	ns	ns	ns
		Saxifraga foliolosa	0.88	ns	ns	ns
		Saxifraga hieracifolia	0.59	ns	ns	ns
		Saxifraga hirculus	.	-5.13	.	ns
		Stellaria laeta	.	-4.21	0.46	ns
	Gram.	**All**	**0.83**	**-1.60**	**0.59**	**ns**
		Carex stans	1.12	-2.43	1.08	ns
		Dupontia fisheri	0.88	ns	0.65	-0.44
		Eriophorum russeolum	.	.	0.36	.
		Eriophorum triste	0.97	-4.09	0.41	ns
		Hierachloë pauciflora	ns	ns	0.62	-0.42
		Juncus biglumis	ns	ns	.	ns
		Luzula arctica	0.67	-2.17	ns	ns
		Luzula confusa	0.79	-4.34	.	ns
		Poa arctica	1.42	ns	ns	ns

Bolded = mean effect size for all species within a given growth form or site
ns = not statistically significant
. *= not enough data to analyze*

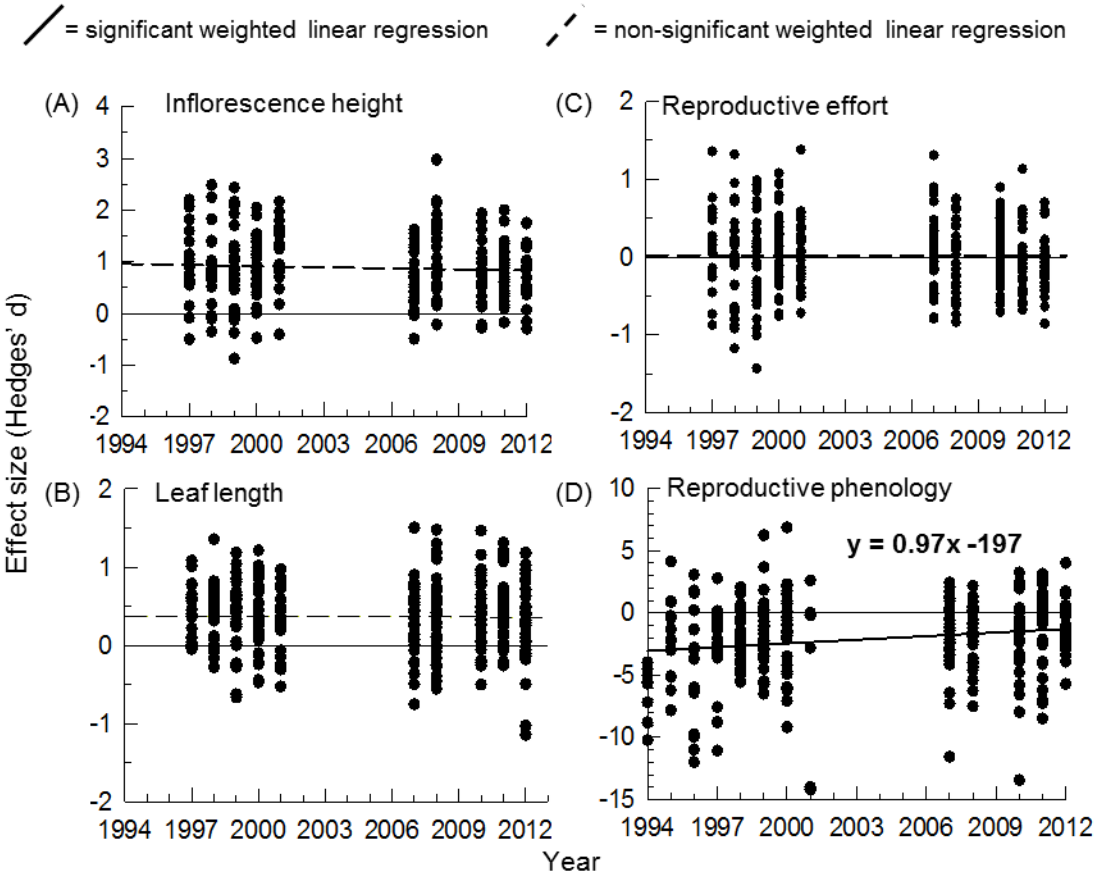


Fig. 4 Relationship between year and effect sizes of experimental warming on plant traits. Traits included: inflorescence height (A), leaf length (B), reproductive effort (C), and reproductive phenology (D). Each point represents the effect size (calculated as Hedges' d) of experimental warming on one plant trait at one study site for a given year. Equations and p values are given for significant weighted least squares regressions (shown with solid line). For reproductive phenology (D) N = 43; for other traits N = 39.

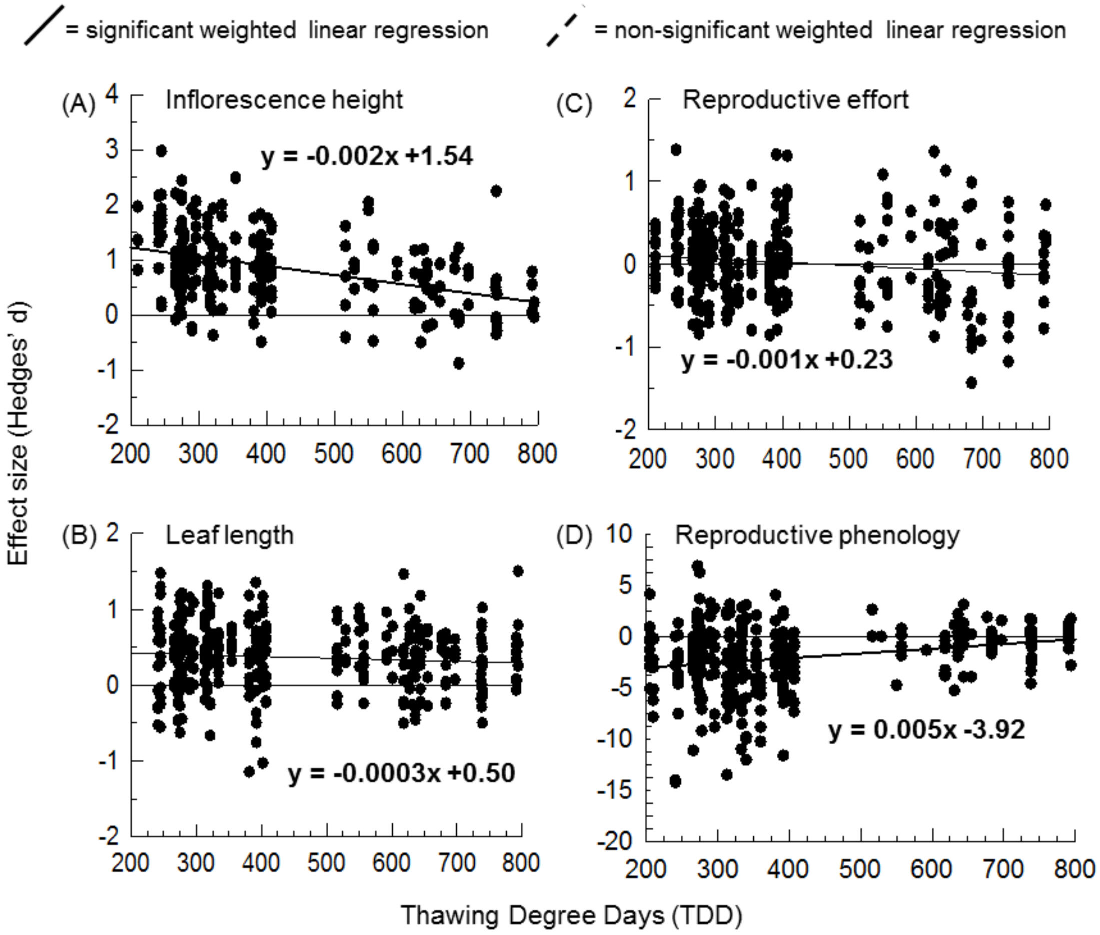


Fig. 5 Relationship between seasonal temperature (TDD) and effect size of experimental warming on plant traits. Traits included: inflorescence height (A), leaf length (B), reproductive effort (C), and reproductive phenology (D). See Fig. 4 for an explanation of the graphs and sample sizes.

Discussion

The results of this study are generally consistent or confirmatory of previous studies. What makes this study unique and of interest is not that the findings are novel, but rather that they are consistent with earlier studies despite the fact that this study has now examined response over 17-19 years of experimental treatment. Thus, this study suggests that the overall response of tundra plants to experimental warming is relatively constant. Like previous studies, the most consistent response to experimental warming observed was an increase in inflorescence heights; this has been observed in earlier studies on the same plots (Hollister et al. 2005a, b) and in previous short-term studies on tundra plants (Arft et al. 1999; Gugerli & Bauert 2001). While few long-term studies report the effects of experimental warming on the inflorescence heights of individual species, other data from long-term studies are consistent with our results, showing that overall plant height increases with warming (Hudson et al. 2011) and that reproductive biomass typically increases with warming (Klady et al. 2011; Campioli et al. 2013).

Experimental warming significantly increased the leaf lengths of many of our plant species equating to an average increase of 9% in total leaf length. Similarly, Dormann & Woodin (2002) found that warming increased plant leaf traits (e.g. size and length) by approximately 15% over a shorter period of time as the studies they included in their analysis had been warmed for typically fewer than 5 years. The overall effect size we report for warming on leaf length over 17-19 years of treatment was also similar to that reported in the earlier short-term study by Arft et al. (1999), which found an effect size of approximately 0.4 during the second and third years of warming treatment. Hudson et al. (2011) reported significant increases in leaf length and size over 16 years of warming in Arctic Canada. Other studies have also noted an increase in photosynthetic biomass and productivity over extended periods of warming (Boelman et al. 2003; Michelsen et al. 2012; Natali et al. 2012). These results, combined with those of our study, suggest that vegetative growth is capable of responding to warming over extended periods of time until temperatures are no longer a limiting factor.

Reproductive phenology typically accelerated with warming, significantly so for 35% of species at our sites. Arft et al. (1999) also found that warming over a short period of time significantly accelerated flowering for many species, resulting in relatively large effect sizes, especially after the first year of treatment. Similar results have been found in earlier studies where warming led to earlier flowering (Dunne et al. 2003; Hollister et al. 2005b) and in numerous observational studies where warmer air temperatures were associated with earlier flowering (Thórhallsdóttir 1998; Post & Forchhammer 2008). However, some studies have also found a delay in flowering date under warmer conditions (Dorji et al. 2013). It should also be noted that some species appear to be reaching a threshold whereby flower timing cannot accelerate further as has been suggested by Iler & Inouye (2013).

Reproductive effort was not typically affected by warming treatment at our sites. Arft et al. (1999) also found that overall reproductive effort was not significantly impacted by warming across a variety of sites over four years of warming. Similar results have been observed in other short-term studies on tundra and sub-alpine plants where effects of warming on reproductive effort showed a high degree of variability between species and years (Lambrecht et al. 2007; Dorji et al. 2013). In contrast to our findings, a long-term study in Arctic Canada (Klady et al. 2011), found that plants exposed to 12 years of warming had significant increases in reproductive effort. Conflicting results between these studies could be explained by the differences in geographic location. Arft et al. (1999) proposed that it would be more beneficial for plants in the High-Arctic to respond to warming with increased reproductive efforts as they presumably faced less competition over resources from their neighbors, reducing the advantage to producing a taller canopy whereas Low-Arctic plants would face such competition and be in need of a more immediate growth response to out-compete neighboring species. Our study was consistent with this hypothesis as our colder sites in Barrow showed significant effect sizes for warming on average inflorescence heights (BD = 0.98, BW = 0.69) and average flowering dates

(BD = -3.84, BW = -1.48) while our relatively warmer sites in Atqasuk did not. Compared to our sites, those examined in Klady et al. (2011) are much farther north and future studies could help discern whether these differences are plastic responses to environmental factors or genetic adaptations within different ecotypes.

Plant responses to warming remained largely consistent over the study period. However, reproductive phenology showed a significant trend toward reduced responses to warming over time and we noted that, although non-significant, regression analyses of our other plant traits were consistent with a diminishing experimental warming response over time (Fig. 4). The general warming trend of the region is the likely explanation for this trend toward a diminished magnitude of response over time given the strong evidence that the effect of warming on plant traits decreases with warming ambient conditions. In other words, plants respond less to experimental warming in warmer years and the later years of the study were generally warmer. Earlier studies (Chapin et al. 1995; Arft et al. 1999) anticipated, and found evidence of, transient warming responses whereby plants initially responded to warming through an increase in growth and reproduction followed by a greatly diminished response. This pattern was expected because arctic plants are adapted to respond to improved summer conditions through accelerated growth and reproduction, at the cost of resources in underground storage (Shaver & Kummerow 1992). However, warmed plants at sites with low average temperatures and high inter-annual variability could still be receiving the recovery time necessary to replenish their nutrient and carbohydrate stores during cooler years, utilizing these stores during warmer years. This could explain discrepancies between our results and those of transplant studies where plants in drastically and consistently warmer conditions may not have adequate time to replenish resources.

Given that the magnitude of warming response showed a much stronger trend with seasonal temperature than the duration of experimental warming, we conclude that plants are able to sustain their responses to warming for longer periods of time than previously suggested. Yet, we also note that temperatures are nearing thresholds where other factors will become limiting. Therefore, we forecast that plants at our sites will shift from being temperature-limited to being constrained by other abiotic factors as the region warms due to climate change. This may already be the case for reproductive phenology at our sites and suggests that some plant species are reaching a threshold in warm years where they are incapable of flowering earlier, as Iler & Inouye (2013) have proposed.

While we present evidence that summer growing temperatures will become less limiting for plant growth and reproduction over time, we have yet to quantify the impacts of abiotic conditions during the winter and spring seasons, both of which can dramatically affect plant species during the growing season (Starr et al. 2000; Bokhurst et al. 2008). Previous studies from other regions in the Arctic indicate that plants at our sites will likely shift from being temperature-limited to being more nutrient and competition-limited (Chapin & Shaver 1985b; Dormann & Woodin 2002). Beyond seasonal weather, nutrient availability, and competition, we recognize that many arctic ecotypes are likely to face limitations brought on by genetic constraints making them less able to respond to what would otherwise be considered more favorable growing conditions (Starr et al. 2000; Mazer et al. 2013). Future studies across a greater range of time, latitudes, and experimental treatments would help establish the relative importance each of these biotic and abiotic factors has on plant species, ultimately improving our ability to predict and understand the impacts of climate change in tundra ecosystems.

The response of plants documented here has complex implications for energy balance, community compositions, and trophic interactions. For example, as plants grow taller and increase canopy complexity they absorb more energy, which will further accelerate warming (Chapin et al. 2000). However, increasing canopy complexity may also enhance the insulating effect of the vegetation layer, in some cases cooling soils and may stabilize permafrost (Hollister et al. 2008). Changes in plant species composition will subsequently influence decomposition rates, in turn affecting carbon and nutrient cycling (Aerts 2006). Changes in plant phenology, growth and community compositions will affect quality and availability of food for herbivores and pollinators, a phenomenon that has already been documented in some parts of the Arctic (Post & Forchhammer 2008; Gilg et al. 2009; Gauthier et al. 2013). Thus future work to link the results of studies on the traits of individual species to shifts in community composition will prove highly useful in better forecasting and understanding changes in the Arctic due to climate change.

CHAPTER III: ARCTIC PLANT RESPONSES TO CHANGING ABIOTIC FACTORS IN NORTHERN ALASKA

Introduction

Climate change is impacting terrestrial ecosystems worldwide and the Arctic has been warming faster and with greater magnitude than other regions (ACIA 2004; IPCC 2013). Recent changes in the Arctic include earlier snowmelts, longer growing seasons, warmer temperatures, and increasing thaw depths (ACIA 2004). Tundra vegetation has begun responding to these shifts through altered plant growth and phenology, north-ward expansion of shrubs and trees, and altered community compositions (ACIA 2004; Tape et al. 2006; Elmendorf et al. 2012a). As arctic plants continue responding to climate change, the effects could have repercussions on ecosystem energy balance, carbon and nutrient cycling, and trophic interactions (Chapin et al. 2005; Aerts 2006; Post & Forchhammer 2008). Because arctic plants play critical roles in regulating these systems, understanding their responses to warming is crucial for predicting the effects of climate change on the Arctic.

While large-scale studies using satellite data and repeat photography have been useful in detecting vegetation change, small-scale studies are easier to experimentally manipulate to examine potential causes (Fraser et al. 2013). Since the 1980’s several long-term research sites have been established in tundra ecosystems making this type of analysis now possible (Chapin et al. 1995; Arft et al. 1999; Dunne et al. 2003; Molau et al. 2005). Such studies have demonstrated that arctic plants respond to both the direct and indirect effects of warming, including accelerated snowmelt, extended growing season length, warmer soils, increased nutrient availability, and increased thaw depth. In general, these effects tend to increase plant growth and accelerate phenology, but responses are often species and site-specific, making accurate predictions difficult (Walker et al. 1994; Arft et al. 1999; Shaver & Jonasson 1999; Hollister et al. 2005a; Oberbauer et al. 2013). Thus, further work is needed to characterize the relationships between arctic plants and abiotic factors if we are to improve our ability to predict how climate change will affect the Arctic.

Using data from long-term research sites in Northern Alaska, we investigated the following questions:

1. How have abiotic factors and plant traits changed over time at these sites?
2. Is there evidence that shifts in abiotic factors could be driving changes in plant traits?

Methods

STUDY SITES AND EXPERIMENTAL DESIGN

This study took place at field sites near Barrow (71°18' N, 156°40' W) and Atqasuk (70°29' N, 157°25' W), Alaska. We collected data from two sites at each location—one in dry heath tundra and the other in wet meadow tundra. The Barrow Dry (BD) and Barrow Wet (BW) sites were established in 1994 and 1995, respectively, while both the Atqasuk Dry (AD) and Atqasuk Wet (AW) sites were established in 1996. For this analysis we focused on abiotic factors collected from 1999-2010 and plant traits collected from 1999, 2000, 2001, 2007, 2008, and 2010 as these were years when all measures of interest were collected. Each site included 48 permanently established plots of vegetation (~1 m^2), half of which were experimentally warmed using Open Top Chambers (OTC’s, Marion et al. 1997). For this study we exclusively focused on plant data from control plots to establish models, referring only to the experimentally warmed plots in order to compare our results in this study with those presented in a separate study at the same sites (Barrett & Hollister in press). The sites used for this study are part of the International Tundra

Experiment (ITEX) and have been previously described in more detail in Hollister et al. (2005a, b). Both locations have a deep heritage of research; Barrow was an International Biological Tundra Biome site in the early 1970's (Brown et al. 1980) and Atqasuk was the focus of the Research on Arctic Tundra Environments (Batzli 1980).

ABIOTIC FACTOR MEASUREMENTS

At each site we collected information on the following abiotic factors: thaw depth, snowmelt date, freeze-up date, growing season length, and air and soil temperatures. Thaw depth values were collected at the end of the summer in each plot within a study site, then averaged for that site each year. We defined snowmelt date as the average date at which each plot was free of snow. When researchers were not present to witness the date of snowmelt, we used the day average soil surface temperatures rose above 0 °C at the site (in most years the numbers were within a few days because snow melt occurs quickly at the site; unpublished data). Freeze-up date was defined as the day of year soil temperatures at 10 cm depth dropped and remained below 0 ºC. Growing season length was calculated as the number of days between snowmelt and freeze-up. Soil moisture was measured hourly at approximately 10 cm below surface (Vitel HYD-10-A - Stevens Vitel Hydrological and Meteorological Systems, Chantilly, VA). All temperatures were recorded hourly with sensors placed approximately 10 cm above ground level and 10 cm below soil surface (recordings varied between the following probes: Hobo H8 Pro – Onset Computer Corporation, Pocasset, MA; Model 107 Temperature Probe – Campbell Scientific Inc., Logan, UT; and MRC TP101M Temperature Probes - Measurement Research Corporation, Gig Harbor, WA). During the 1999-2001 field seasons, early season air temperatures were missing from snowmelt until loggers were placed (up to 9 days after snowmelt but typically fewer than 5 days). These missing temperatures were estimated using climate tower readings from the dry sites (Barrett & Hollister in press). We expressed temperatures as degree days from snowmelt, which were calculated using the following method: subtracting a base temperature (either -7 °C, -5 °C, -2 °C, 0 °C, 2 °C, or 5 °C) from an average daily temperature, then summing positive values over the period of interest. This period varied depending on the plant trait examined. For comparison with leaf lengths, inflorescence heights, and reproductive efforts, degree day sums were calculated above and below ground for the duration of the summer (snowmelt date through August 15) or fall (August 15 through freeze-up date). For comparison with reproductive phenology, we determined the average day of flower or inflorescence burst for each species across all years and then summed degree days from snowmelt until this day of year.

PLANT TRAIT MEASUREMENTS

Within each plot we measured the following plant traits for most species: inflorescence height, leaf length, reproductive effort, and reproductive phenology. These traits were chosen based on their reproducibility across species with minimal effort so that measurements could be sustained over many years. They were chosen as proxies designed to inform us about changes in plant reproductive effort, plant growth, and phenology; they also conform with protocols used for cross biome synthesis (Arft et al. 1999). We measured inflorescence height from the ground to the top of an inflorescence in forbs and graminoids and the distance from the inflorescence base to tip in shrubs. Similarly, we measured leaf lengths from the base of a plant to the tip of its tallest leaf in graminoids and forbs, with the exception of *Potentilla hyparctica* and *Stellaria laeta*, where we used the distance from the base of the longest leaf to the tip of that leaf. This method was also used for shrubs. Leaf length for *Cassiope tetragona* refers to length of its most recent annual growth increment (Callaghan et al. 1989; Johnstone & Henry 1997). For inflorescence height and leaf length we used maximum size reached by an individual plant during the summer growing period (snowmelt to August 15). Inflorescence heights and leaf lengths were averaged for each plot using one to six individuals (typically fewer than three), depending on the abundance of the species in that plot. Measurements were made on up to three permanently marked individuals per plot. In many cases markers were lost between years and new individuals were randomly chosen. Measurements were also made on the three largest reproductive individuals within a plot. The morphology of a species determined whether we used flower or inflorescence measurements to represent the reproductive effort and flowering date of that species. Reproductive effort was defined as either the total number of inflorescences or flowers produced by a species over the season. Reproductive phenology was determined as either the first day of year an inflorescence appeared in a plot or as the first day of year when anthers or stigmas became clearly visible in a plot. We observed flowering date, inflorescence number, and flower number in each plot one to three times per week, the only exception being in 2001 when only ten plots of each treatment type were observed for all plant traits due to logistical constraints.

STATISTICAL ANALYSES

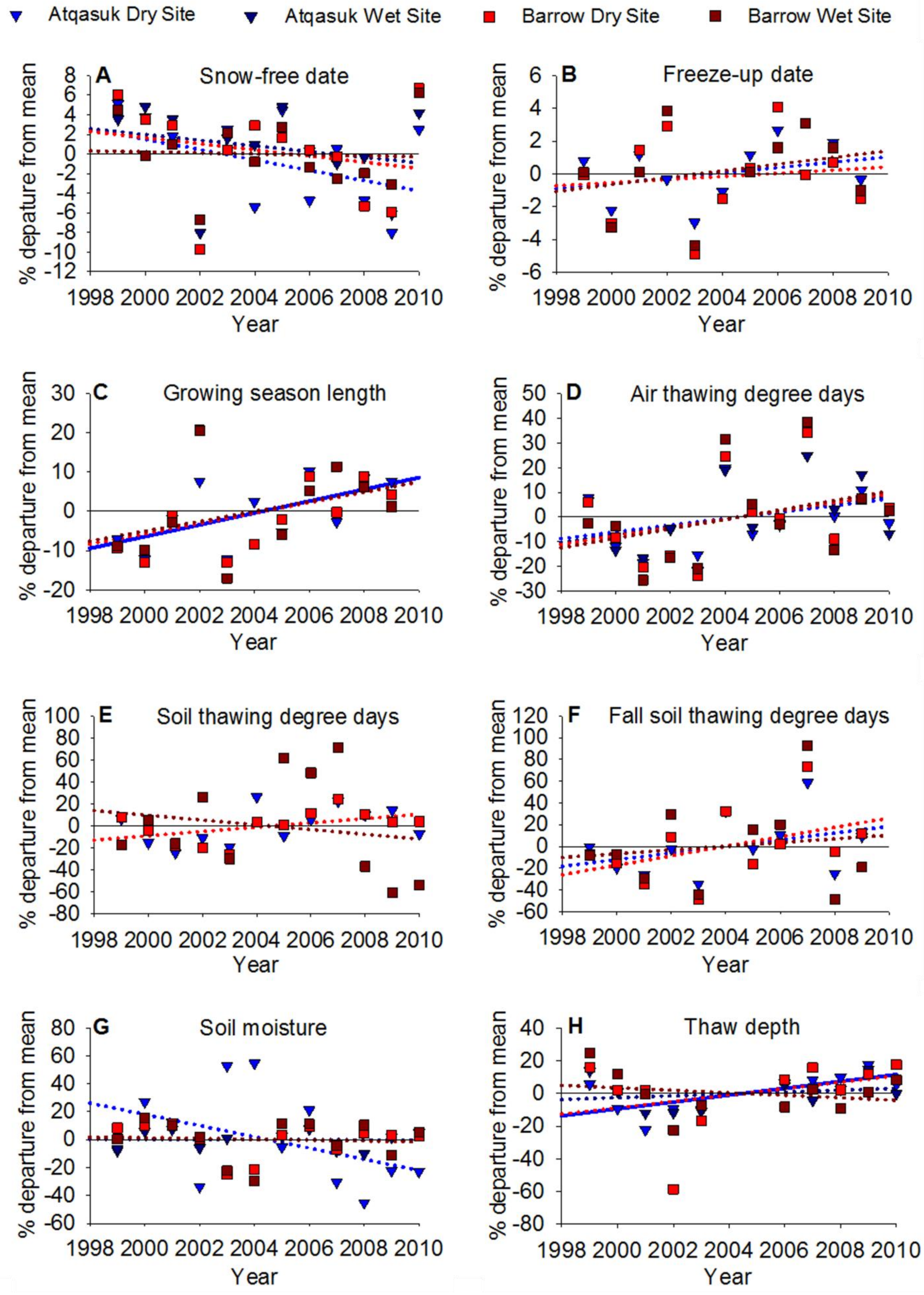
Trends in abiotic factors over time were examined using linear regressions in Program R (R Development Core Team 2005). To determine if the traits of individual species had changed over time we used linear mixed models (LMM's) using a Gaussian error distribution where we treated year as a fixed effect and plot and year as random effects. These tests were performed using the lme4 package in Program R (Bates et al. 2015). To determine whether a trait showed a significant trend over time, a chi-squared likelihood ratio test was performed between models with and without time as an explanatory variable ($\alpha = 0.05$) in the Program R (R Development Core Team 2005). To relate traits of a species to each abiotic factor of interest we also used LMM's with the abiotic factor of interest as a fixed effect and plot and year as random effects. We then used a chi-squared likelihood ratio test to compare models with and without time as an explanatory variable and applied the Benjamini-Hochberg procedure to control the false discovery rate at 5% for each species. To be included in the analysis, a species had to be present in at least five plots of each treatment at a site and at least four years of study; ten species met this criteria at the AD site, six at the AW site, fourteen at the BD site, and seventeen at the BW site. For simplicity we counted male and female populations of *Salix* as separate species (*Salix* was only abundant at the BD site). We considered abiotic factors during the year plant traits were collected as well as the year previous to collection.

Results

TRENDS IN ABIOTIC FACTORS AND PLANT TRAITS IN OUR SITES

The only significant trends were toward deeper thaw depths and longer growing seasons over time at the AD site (Fig. 6). However, most abiotic factors showed non-significant tendencies consistent with a warming Arctic (Fig. 6); these included non-significant tendencies toward earlier snowmelt, later freeze up, longer growing season, greater thawing degree day accumulations of air and soils, drier soils and deeper thaw at all sites where recordings were made except at the BW site where soil thawing degree days and thaw depth showed a non-significant decrease over time. At the AW site there was an instrument malfunction and as a result the following are not reported: freeze up date, growing season length, soil thawing degree days, and fall soil thawing degree days.

Traits of a few species showed significant trends over time (Fig. 7). For 9% of the plant species we found trends toward taller inflorescences over time while 6% trended toward shorter inflorescences over time (percentages were calculated by counting all the species at a site that showed a significant relationship after applying the Benjamini-Hochberg procedure and dividing by the total). 2% of plant species trended toward increasing reproductive efforts over time while 2% the opposite. Leaf lengths trended toward shorter leaves in 18% of our plant species, with 2% trending in the opposite direction. We found no significant trends in reproductive phenology over time.



Atqasuk Dry Site
Atqasuk Wet Site
Barrow Dry Site
Barrow Wet Site
A
Snow-free date
B
Freeze-up date
C
Growing season length
D
Air thawing degree days
E
Soil thawing degree days
F
Fall soil thawing degree days
G
Soil moisture
H
Thaw depth
% depature from mean
% departure from mean
Year
1998
2000
2002
2004
2006
2008
2010

Fig. 6 Trends in abiotic factors at each study site over time including (A) Snow free date, (B) Freeze-up date, (C) Growing season length, (D) Air thawing degree days, (E) Soil thawing degree days, (F) Fall soil thawing degree days, (G) Soil moisture, and (H) Thaw depth. Each point represents the percent departure each year from the average over the course of the study. Significant trends from linear regressions are shown as solid lines while non-significant tendencies are shown as dashed lines. Further details for each abiotic factor are discussed in Methods section. See Appendix 1 in Barrett et al. 2015 for the mean values of all factors and Appendix 2 in Barrett et al. 2015 for details on each analysis.

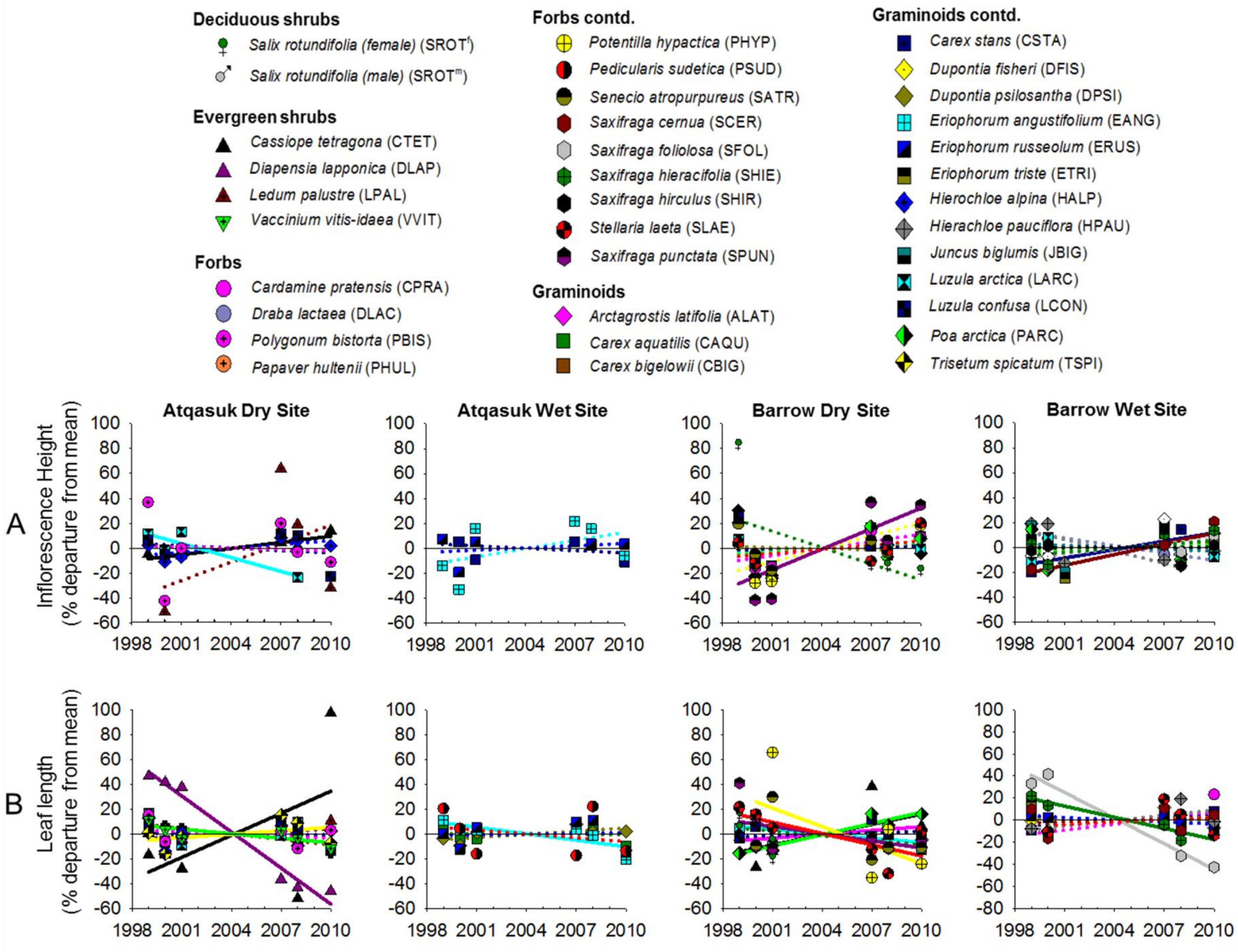

Deciduous shrubs
Salix rotundifolia (female) (SROT^f)
Salix rotundifolia (male) (SROT^m)
Evergreen shrubs
Cassiope tetragona (CTET)
Diapensia lapponica (DLAP)
Ledum palustre (LPAL)
Vaccinium vitis-idaea (VVIT)
Forbs
Cardamine pratensis (CPRA)
Draba lactaea (DLAC)
Polygonum bistorta (PBIS)
Papaver hultenii (PHUL)
Forbs contd.
Potentilla hypactica (PHYP)
Pedicularis sudetica (PSUD)
Senecio atropurpureus (SATR)
Saxifraga cernua (SCER)
Saxifraga foliolosa (SFOL)
Saxifraga hieracifolia (SHIE)
Saxifraga hirculus (SHIR)
Stellaria laeta (SLAE)
Saxifraga punctata (SPUN)
Graminoids
Arctagrostis latifolia (ALAT)
Carex aquatilis (CAQU)
Carex bigelowii (CBIG)
Graminoids contd.
Carex stans (CSTA)
Dupontia fisheri (DFIS)
Dupontia psilosantha (DPSI)
Eriophorum angustifolium (EANG)
Eriophorum russeolum (ERUS)
Eriophorum triste (ETRI)
Hierochloe alpina (HALP)
Hierachloe pauciflora (HPAU)
Juncus biglumis (JBIG)
Luzula arctica (LARC)
Luzula confusa (LCON)
Poa arctica (PARC)
Trisetum spicatum (TSPI)
Atqasuk Dry Site
Atqasuk Wet Site
Barrow Dry Site
Barrow Wet Site
A
Inflorescence Height (% departure from mean)
100
80
60
40
20
0
-20
-40
-60
1998
2001
2004
2007
2010
B
Leaf length (% departure from mean)
100
80
60
40
20
0
-20
-40
-60
-80
1998
2001
2004
2007
2010

Fig. 7 contd.

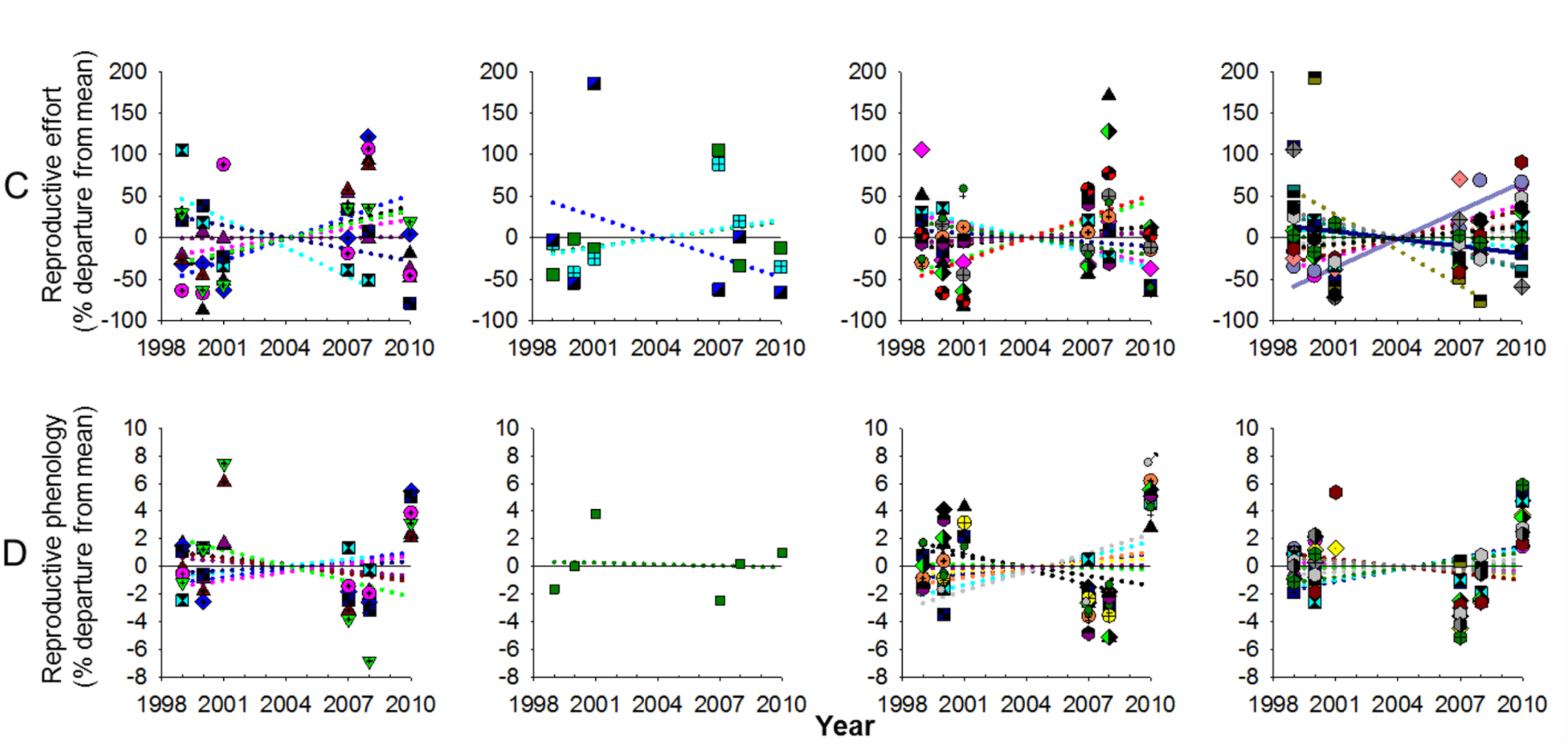

C
Reproductive effort
(% departure from mean)
200
150
100
50
0
-50
-100
1998
2001
2004
2007
2010
D
Reproductive phenology
(% departure from mean)
10
8
6
4
2
0
-2
-4
-6
-8
Year

Fig. 7 Trends in plant traits as each study site over time including (A) Inflorescence height, (B) Leaf length, (C) Reproductive effort, and (D) Reproductive phenology. Each point represents the percent departure each year for a species from its average value over the course of the study. Significant trends from linear mixed model (LMM) are shown as solid lines while non-significant tendencies are shown as dashed lines. Further details for each plant trait and statistical procedures are discussed in Methods section. See Appendix 3 in Barrett et al. 2015 for the mean values of all plant traits and Appendix 4 in Barrett et al. 2015 for details on each analysis.

RELATIONSHIPS BETWEEN ABIOTIC FACTORS AND PLANT TRAITS AT OUR SITES

Several abiotic factors showed strong relationships with plant traits at our sites, but air and soil temperatures were correlated with the greatest number of species across all traits (Fig. 8). Generally, warmer temperatures were associated with taller inflorescences, increased reproductive efforts, earlier flowering, and longer leaves. The same plant trait characteristics were also typically associated with greater thaw depths, earlier snowmelts, and longer previous year growing seasons. Drier soils were associated with earlier flowering, shorter leaves and inflorescences, and decreased reproductive efforts.

While abiotic factors from the current year were typically able to predict a greater number of species responses (and with higher R^2 values) than abiotic factors from the previous year, this was not always the case. For several species, the conditions during the previous season were just as predictive, if not more predictive, than those during the current season. For example, at the BD site, reproductive effort for *Cassiope tetragona* could not be predicted using air temperatures from the current season, but could be instead using air temperatures from the previous season (Fig. 9). Similarly, abiotic factors from the previous year were the best predictors for reproductive efforts in *Stellaria laeta*, *Arctagrostis latifolia* and *Poa arctica* at the BD site, and *Hierochloe alpina* at the AD site.

Varying the degree day base temperature also altered which species were significantly predicted and the strength of the correlation for each trait we examined (Fig. 10). For example, inflorescence height of *Poa arctica* was best predicted with a degree day base of 2 °C, as opposed to the more common threshold used in tundra vegetation studies of 0 °C (Fig. 11). Generally, the traits of species in the cooler Barrow sites were better predicted using degree days with lower base temperatures while the opposite was true of species in the warmer Atqasuk sites. For example, at Barrow, 55% of the species that showed significant relationships with air temperatures showed their highest R^2 values using degree days with a base below zero while no plants in Atqasuk showed this relationship. Furthermore, 60% of Atqasuk species showed the highest R^2 values for degree days with bases above 0 °C while the same was true for only 11% of species in Barrow. In examining traits across sites, we observed that generally degree days with lower base temperatures better predicted the leaf lengths of species while the opposite was true for inflorescence heights.

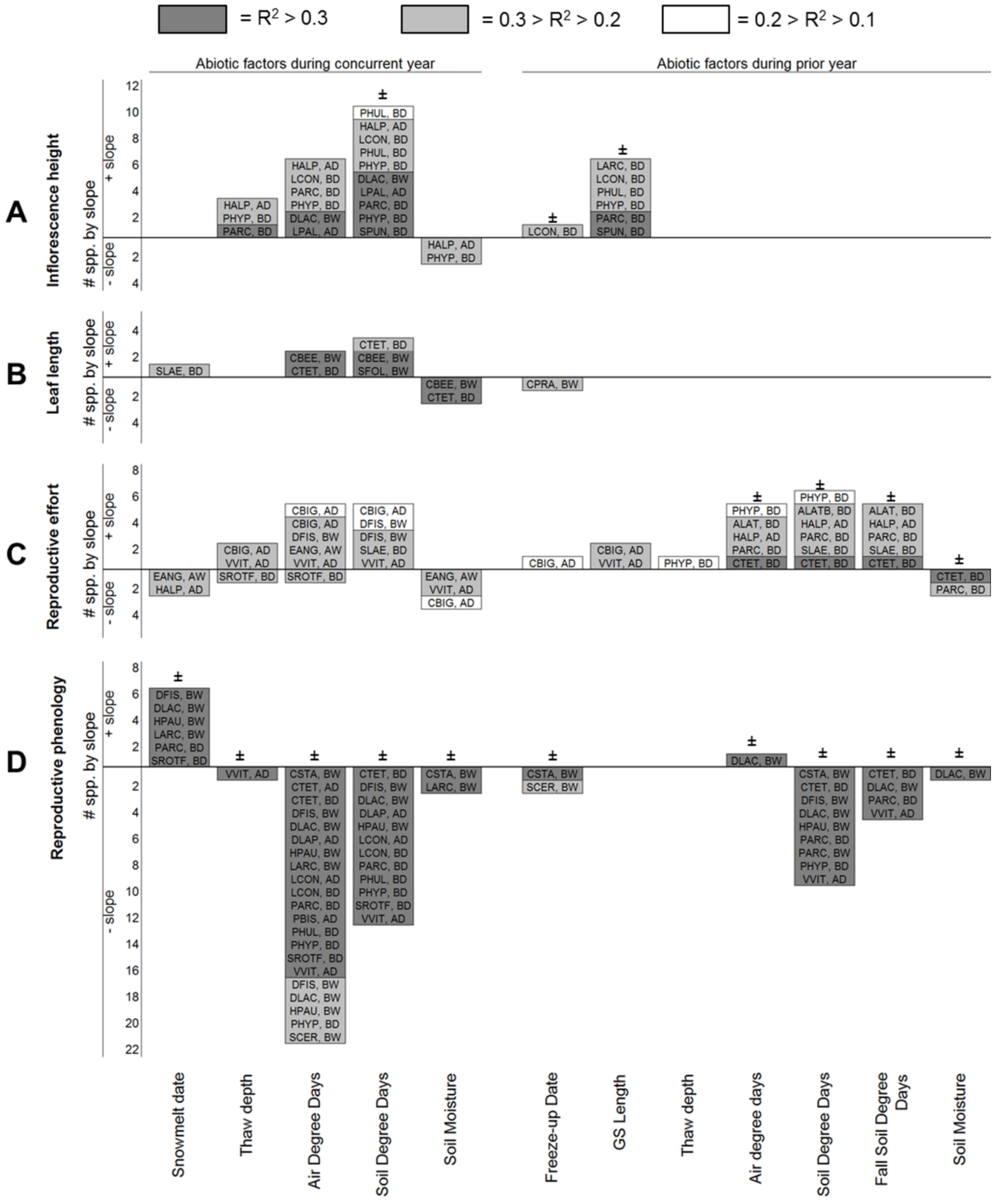

= R² > 0.3
= 0.3 > R² > 0.2
= 0.2 > R² > 0.1
Abiotic factors during concurrent year
Abiotic factors during prior year
A
Inflorescence height
B
Leaf length
C
Reproductive effort
D
Reproductive phenology
spp. by slope
+ slope
- slope
PHUL, BD
HALP, AD
LCON, BD
PHUL, BD
PHYP, BD
DLAC, BW
LPAL, AD
PARC, BD
PHYP, BD
SPUN, BD
HALP, AD
LCON, BD
PARC, BD
PHYP, BD
DLAC, BW
LPAL, AD
HALP, AD
PHYP, BD
PARC, BD
HALP, AD
PHYP, BD
LCON, BD
LARC, BD
LCON, BD
PHUL, BD
PHYP, BD
PARC, BD
SPUN, BD
±
SLAE, BD
CBEE, BW
CTET, BD
CTET, BD
CBEE, BW
SFOL, BW
CBEE, BW
CTET, BD
CPRA, BW
EANG, AW
HALP, AD
CBIG, AD
VVIT, AD
SROTF, BD
CBIG, AD
CBIG, AD
DFIS, BW
EANG, AW
VVIT, AD
SROTF, BD
CBIG, AD
DFIS, BW
DFIS, BW
SLAE, BD
VVIT, AD
EANG, AW
VVIT, AD
CBIG, AD
CBIG, AD
CBIG, AD
VVIT, AD
PHYP, BD
PHYP, BD
ALAT, BD
HALP, AD
PARC, BD
CTET, BD
PHYP, BD
ALATB, BD
HALP, AD
PARC, BD
SLAE, BD
CTET, BD
ALAT, BD
HALP, AD
PARC, BD
SLAE, BD
CTET, BD
CTET, BD
PARC, BD
DFIS, BW
DLAC, BW
HPAU, BW
LARC, BW
PARC, BD
SROTF, BD
VVIT, AD
CSTA, BW
CTET, AD
CTET, BD
DFIS, BW
DLAC, BW
DLAP, AD
HPAU, BW
LARC, BW
LCON, AD
LCON, BD
PARC, BD
PBIS, AD
PHUL, BD
PHYP, BD
SROTF, BD
VVIT, AD
DFIS, BW
DLAC, BW
HPAU, BW
PHYP, BD
SCER, BW
CTET, BD
DFIS, BW
DLAC, BW
DLAP, AD
HPAU, BW
LCON, AD
LCON, BD
PARC, BD
PHUL, BD
PHYP, BD
SROTF, BD
VVIT, AD
CSTA, BW
LARC, BW
CSTA, BW
SCER, BW
DLAC, BW
CSTA, BW
CTET, BD
DFIS, BW
DLAC, BW
HPAU, BW
PARC, BD
PARC, BW
PHYP, BD
VVIT, AD
CTET, BD
DLAC, BW
PARC, BD
VVIT, AD
DLAC, BW
Snowmelt date
Thaw depth
Air Degree Days
Soil Degree Days
Soil Moisture
Freeze-up Date
GS Length
Thaw depth
Air degree days
Soil Degree Days
Fall Soil Degree Days
Soil Moisture

Fig. 8 Relationships between plant traits and abiotic factors. The following plant traits were included: (A) Inflorescence height, (B) Leaf length, (C) Reproductive effort, and (D) Reproductive phenology. Each bar represents a species from a site that showed a significant LMM where abiotic factors were considered fixed effects while plot and year were treated as random effects. The number of species for which models were run was between 35-40 unless denoted (± represents 27-34). Significance levels were independently determined for each species using the Benjamini-Hochberg procedure with a 5% false discovery rate following a Pearson chi-square likelihood test. For a description of the abiotic factors see Fig. 6 and for the species codes see Fig. 7. Site abbreviations are as follows: Atqasuk Dry (AD), Atqasuk Wet (AW), Barrow Dry (BD) and Barrow Wet (BW). For further details regarding LMM's results refer to Appendices 8 and 9 in Barrett et al. 2015.

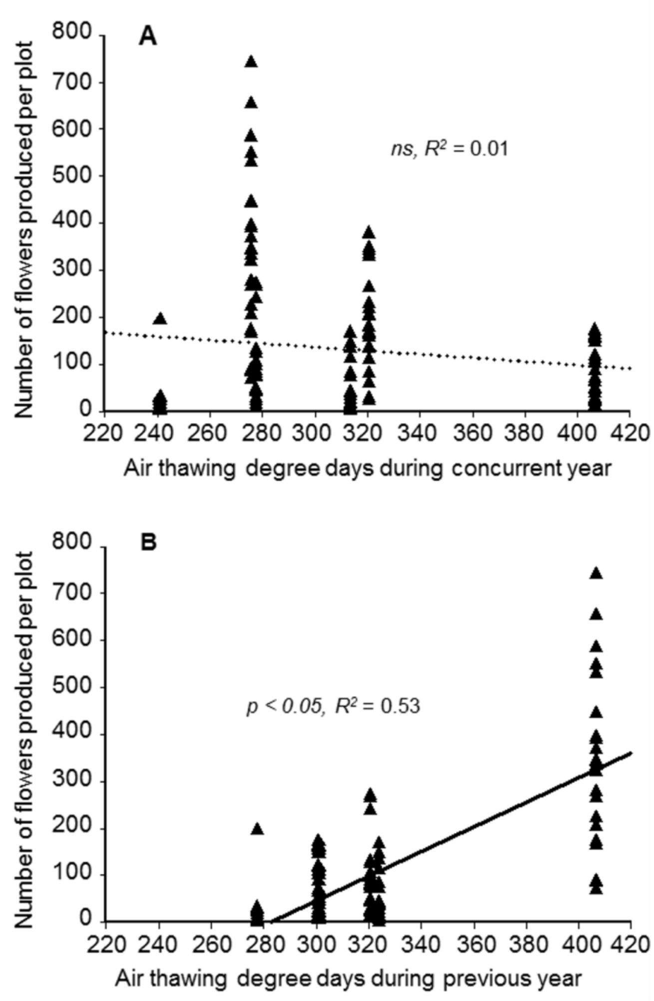


Fig. 9 Comparative ability of thawing degree days to predict reproductive effort in *Cassiope tetragona* using temperature records from the (A) Current and (B) Prior year. Each point represents the total number of flowers in a plot at the BD site. There was a significant relationship between the number of flowers produced and thawing degree days when using temperature records from the prior field season (denoted with a solid line) but the relationship was not significant when using temperature records of the current year (denoted with a dashed line). For further details regarding LMM results refer to Appendices 8 and 9 in Barrett et al. 2015.

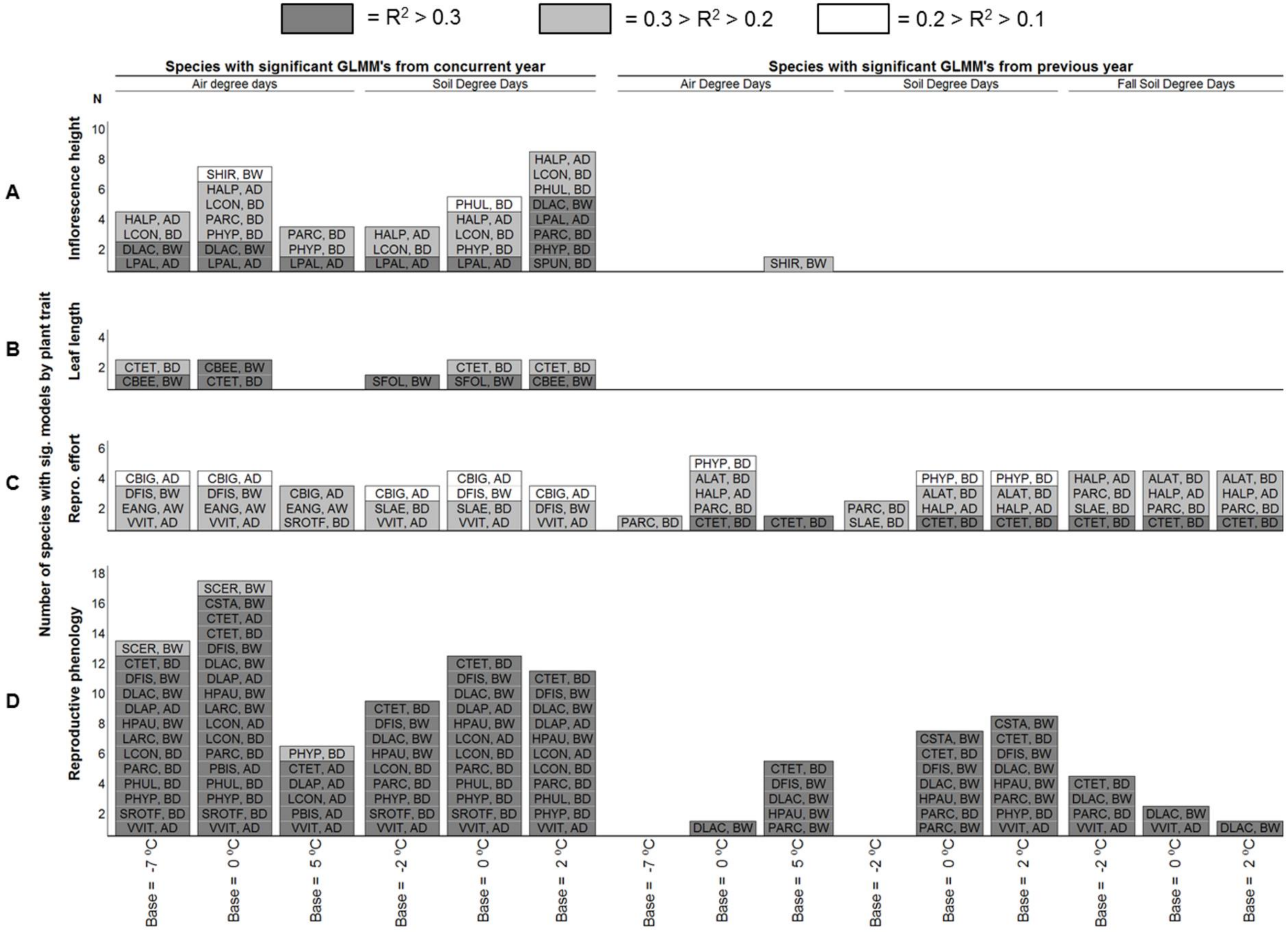

= $R^2 > 0.3$
= $0.3 > R^2 > 0.2$
= $0.2 > R^2 > 0.1$
Species with significant GLMM's from concurrent year
Air degree days
Soil Degree Days
Species with significant GLMM's from previous year
Air Degree Days
Soil Degree Days
Fall Soil Degree Days
N
Number of species with sig. models by plant trait
A
Inflorescence height
10
8
6
4
2
HALP, AD
LCON, BD
DLAC, BW
LPAL, AD
SHIR, BW
HALP, AD
LCON, BD
PARC, BD
PHYP, BD
DLAC, BW
LPAL, AD
PARC, BD
PHYP, BD
LPAL, AD
HALP, AD
LCON, BD
LPAL, AD
PHUL, BD
HALP, AD
LCON, BD
PHYP, BD
LPAL, AD
HALP, AD
LCON, BD
PHUL, BD
DLAC, BW
LPAL, AD
PARC, BD
PHYP, BD
SPUN, BD
SHIR, BW
B
Leaf length
4
2
CTET, BD
CBEE, BW
CBEE, BW
CTET, BD
SFOL, BW
CTET, BD
SFOL, BW
CTET, BD
CBEE, BW
C
Repro. effort
6
4
2
CBIG, AD
DFIS, BW
EANG, AW
VVIT, AD
CBIG, AD
DFIS, BW
EANG, AW
VVIT, AD
CBIG, AD
EANG, AW
SROTF, BD
CBIG, AD
SLAE, BD
VVIT, AD
CBIG, AD
DFIS, BW
SLAE, BD
VVIT, AD
CBIG, AD
DFIS, BW
VVIT, AD
PARC, BD
PHYP, BD
ALAT, BD
HALP, AD
PARC, BD
CTET, BD
CTET, BD
PARC, BD
SLAE, BD
PHYP, BD
ALAT, BD
HALP, AD
CTET, BD
PHYP, BD
ALAT, BD
HALP, AD
CTET, BD
HALP, AD
PARC, BD
SLAE, BD
CTET, BD
ALAT, BD
HALP, AD
PARC, BD
CTET, BD
ALAT, BD
HALP, AD
PARC, BD
CTET, BD
D
Reproductive phenology
18
16
14
12
10
8
6
4
2
SCER, BW
CTET, BD
DFIS, BW
DLAC, BW
DLAP, AD
HPAU, BW
LARC, BW
LCON, BD
PARC, BD
PHUL, BD
PHYP, BD
SROTF, BD
VVIT, AD
SCER, BW
CSTA, BW
CTET, AD
CTET, BD
DFIS, BW
DLAC, BW
DLAP, AD
HPAU, BW
LARC, BW
LCON, AD
LCON, BD
PARC, BD
PBIS, AD
PHUL, BD
PHYP, BD
SROTF, BD
VVIT, AD
PHYP, BD
CTET, AD
DLAP, AD
LCON, AD
PBIS, AD
VVIT, AD
CTET, BD
DFIS, BW
DLAC, BW
HPAU, BW
LCON, BD
PARC, BD
PHYP, BD
SROTF, BD
VVIT, AD
CTET, BD
DFIS, BW
DLAC, BW
DLAP, AD
HPAU, BW
LCON, AD
LCON, BD
PARC, BD
PHUL, BD
PHYP, BD
SROTF, BD
VVIT, AD
CTET, BD
DFIS, BW
DLAC, BW
DLAP, AD
HPAU, BW
LCON, AD
LCON, BD
PARC, BD
PHUL, BD
PHYP, BD
VVIT, AD
DLAC, BW
CTET, BD
DFIS, BW
DLAC, BW
HPAU, BW
PARC, BW
CSTA, BW
CTET, BD
DFIS, BW
DLAC, BW
HPAU, BW
PARC, BD
PARC, BW
CSTA, BW
CTET, BD
DFIS, BW
DLAC, BW
HPAU, BW
PARC, BW
PHYP, BD
VVIT, AD
CTET, BD
DLAC, BW
PARC, BD
VVIT, AD
DLAC, BW
VVIT, AD
DLAC, BW
Base = -7 °C
Base = 0 °C
Base = 5 °C
Base = -2 °C
Base = 0 °C
Base = 2 °C
Base = -7 °C
Base = 0 °C
Base = 5 °C
Base = -2 °C
Base = 0 °C
Base = 2 °C
Base = -2 °C
Base = 0 °C
Base = 2 °C

Fig.10 Comparative abilities of degree days calculated with different base temperatures to predict plant traits. Plant traits include (A) Inflorescence length, (B) Leaf length, (C) Reproductive effort, and (D) Reproductive phenology. Each bar represents one species showing a significant relationship with a given abiotic factor determined using LMM's. Formatting follows Fig. 8 except slope sign is not indicated. Degree day base temperatures are indicated as "Base = X ^{0}C", with varying "X" values; for simplicity we only present a subset of the base values, for the complete results see Appendix 6 in Barrett et al. 2015. Significance levels were independently determined for each species using the Benjamini-Hochberg method with a 5% false discovery rate. For further details regarding LMM results refer to Appendices 5 and 6 in Barrett et al. 2015.

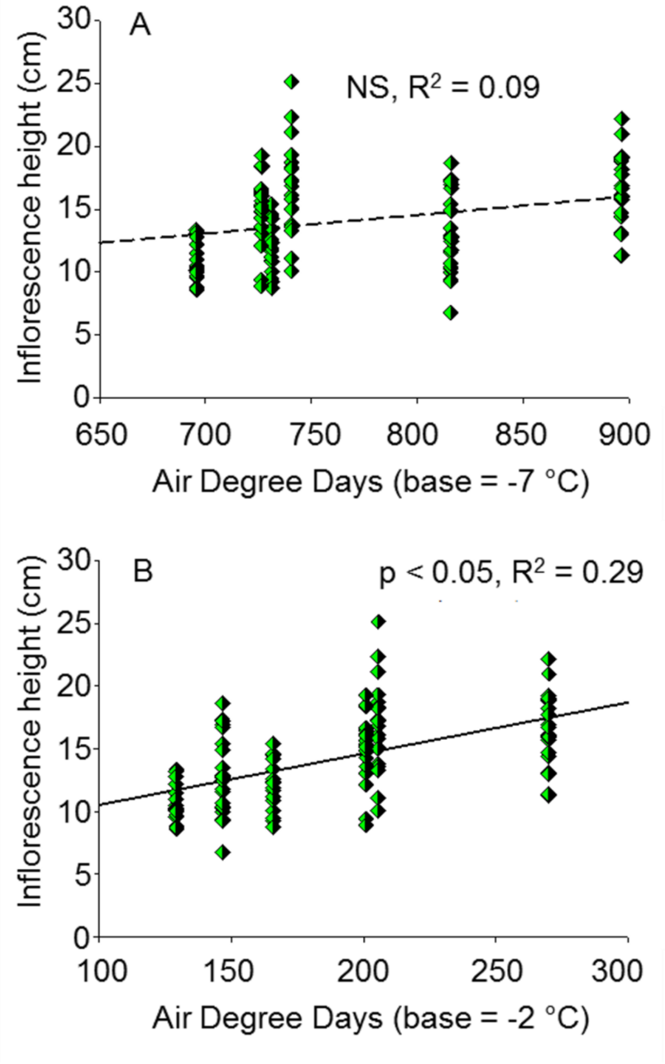


Fig. 11 Predicting *Poa arctica* inflorescence heights using different degree day base temperatures. Shown are the results of LMM's comparing inflorescence height to degree days of base temperatures of (A) -7 °C and (B) 2 °C. Each point represents average inflorescence height within a plot at the Barrow Dry site. There was a significant relationship between degree days and inflorescence height when using a base temperature of 2 °C (denoted with a solid line) but the relationship was not significant when using a base temperature of -7 °C (denoted with a

dashed line). For further details regarding LMM results refer to Appendices 8 and 9 in Barrett et al. 2015.

Discussion

ABIOTIC FACTORS AT OUR SITES ARE CHANGING IN A MANNER CONSISTENT WITH CLIMATE CHANGE PROJECTIONS

Recent studies on the impacts of climate change on the Arctic have documented warming air and soil temperatures, increasing thaw depths, changing soil hydrology, and accelerating snowmelt along with delaying freeze-ups resulting in longer growing season lengths (Serreze et al. 2000; ACIA 2005; Hinzman et al. 2005). While the findings from this study represent a relatively short time period, tendencies at our sites are comparable to recent climate trends throughout the Arctic. Moreover, they align with local patterns in the North Slope of Alaska (Kittel et al. 2011) and in the Barrow area (Stone et al. 2002; Wendler et al. 2014). At the AD site, growing season length showed a significant trend toward longer summers over time and the active layer trended toward deeper depths over time. Although at the other three sites the tendencies were non-significant, they were all in the same direction (Fig. 6C, F). The increase in growing season length has been occurring through a combination of earlier snow-melt and delayed freeze-up (Fig. 6A, B). These findings are consistent with those of several larger-scale studies using satellite observations, which show a pattern of increased growing season lengths throughout the Arctic, resulting in greener summers for tundra biomes (Stow et al. 2004; Verbyla 2008). In addition to the direct impact of longer summers on tundra flora and fauna (Post et al. 2009), longer growing seasons are driving warming trends throughout the Arctic, including the North Slope of Alaska (Euskirchen et al. 2007; Kittel et al. 2011). Thaw depth is controlled by the complex interactions of soil type, moisture content, and temperature and can show large variation even over short distances and between years (Hinkel & Nelson 2003; Shiklomanov et al. 2010). For these reasons, we had not expected to find significant trends in the active layer depth at any of our sites. The general increase in thaw depth at our sites is likely being caused by increasing air temperatures and earlier snowmelts, which have acted to drain and warm the soils throughout the region (Jorgenson et al. 2006; Akerman & Johansson 2008; Park et al. 2012). The AD site may have demonstrated a stronger trend toward a deeper active layer than the other sites because this site has much warmer soil temperatures and drier soils than our other sites (Appendix 1 in Barrett et al. 2015). We also observed tendencies toward warmer summer air and soil temperatures, warmer fall soil temperatures, and drier soils over time at all fours sites; although there was great variability from year to year and none of these tendencies were statistically significant.

PLANT TRAITS AT OUR SITES SHOW CONSISTENT, ALTHOUGH TYPICALLY NON-SIGNIFICANT TENDENCIES PARALLEL TO THOSE ANTICIPATED WITH CLIMATE CHANGE

The majority of our species showed non-significant tendencies toward increasing inflorescence heights and reproductive efforts over time (Fig. 7) which is consistent with general observations and predictions regarding arctic plant responses to climate change (Arft et al. 1999; Dormann & Woodin 2002; ACIA 2004; Hudson & Henry 2009). Interestingly, 18% of the species at these sites showed significant trends toward decreasing leaf lengths over time, opposite of what was predicted given the overall tendency toward warmer conditions over time at these sites. The trends toward decreasing leaf length could be related to the cumulative and consistent, yet non-significant, tendencies toward increased reproductive efforts and larger inflorescences over time as species shift more resources into reproduction. For example, *Diapensia lapponica* at the

Atqasuk Dry site showed significant trends toward taller inflorescences and shorter leaves over time. However, further study would be needed to test this explanation and could examine how species shift their resources given warmer conditions. This suggests that despite a well-documented tendency for warming to cause tundra plants to grow taller, flower earlier, and produce more flowers (Arft et al. 1999; Dormann & Woodin 2002; Hollister et al. 2005a), other abiotic factors such as resource allocation strategies and responses to soil moisture need to be accounted for in order to develop accurate predictions for vegetation change.

MANY PLANT TRAITS ARE CORRELATED WITH AIR AND SOIL TEMPERATURES

In agreement with previous studies, we found that degree days can provide useful predictions of flowering, growth, and reproduction in arctic plants (Chapin et al. 1995; Thorhallsdottir 1998; Molau et al. 2005; Hoffmann et al. 2010). It is well-documented that warmer temperatures (higher degree days) are often associated with taller inflorescences, longer leaves, earlier flowering dates, and increased reproductive effort in plants (Thorhallsdottir 1998; Arft et al. 1999; Hollister et al. 2005a). Furthermore, experimental warming studies have confirmed that temperature is at least a partial driver of these responses (Arft et al. 1999; Dunne et al. 2003; Marchand et al. 2004; Hollister et al. 2005a; Hudson et al. 2011; Elmendorf et al. 2012b; Klady et al. 2011). The low number of species showing significant trends in their traits over time can likely be explained by the high degree of variability in abiotic factors over the course of the study and that these traits tend to be strongly influenced by these factors. Beyond year to year variability in abiotic factors and plant traits, it appears that other biotic and abiotic factors may be placing stronger limitations on some plant traits, warranting further investigation (Fig. 8). Studies from low Arctic regions provide strong evidence that nutrient limitation is of greater importance than temperature and that there is a synergism between the two (Chapin et al. 1995; Shaver & Jonasson 1999).

MODIFYING DEGREE DAY BASE TEMPERATURES IMPROVED OUR ABILITY TO PREDICT PLANT RESPONSES TO TEMPERATURE

Arctic plants are notorious for their phenotypic plasticity and sometimes demonstrate a greater range of responses between conspecifics at different geographic locations than with other species located in the same area (Stenström et al. 2002; Hollister, et al. 2005a). Thus, we expected to find that varying the base temperature used to calculate degree days would improve predictions more by site and trait than by species. Presumably, plants in the Barrow sites are better suited to growth in lower temperatures than are those in Atqasuk as these sites are generally cooler. Generally zero is used as the basis for degree day predictions in the tundra; however we found that the best base temperature to calculate degree days was not always zero. Most traits of species in Barrow were best predicted with a degree day base below zero while at Atqasuk most traits of species were best predicted with a degree day base above zero. In the future, site-based degree days could become a useful tool for predicting plant responses to climate change. This could be further examined by comparing relative abilities of degree days with varying base temperature between species that occur across multiple sites. While our data offer a limited opportunity to examine this due to the low number of species occurring in multiple sites and showing significant relationships with air and soil temperatures, we do note that the general pattern we observed held true for both *Cassiope tetragona* and *Luzula confusa*.

Selecting the optimal base temperature for predicting a plant trait in response to temperature may also depend on whether the plant trait relates to reproductive or vegetative behavior. Generally, using degree days with lower base temperatures improved predictions of leaf lengths, potentially reflecting the fact that arctic plants are pre-adapted to grow at cold temperatures and that accounting for this by decreasing their presumed growth threshold increases predictability for this trait. The opposite trend was true for reproductive phenology and inflorescence heights, which could be attributed to the fact that sexual reproduction represents a higher caloric cost than vegetative growth and therefore may be less likely to proceed under cooler temperatures. This idea could be tested by first establishing optimal growth conditions for each species within a site and then using a degree day based on this physiological trait to predict how plants will respond to warming. Alternatively, our degree day base temperature adjustments may be reflecting the fact that inflorescence heights would be affected more by late-season temperatures than early-season temperatures and a degree day with a high base temperature would artificially take this into account as late season temperatures are typically higher.

We tested degree days with base temperatures below 0 °C under the assumption that temperatures in the tissues of arctic plants can be significantly warmer than ambient air temperatures (Bliss 1971; Savile 1972) and found 3 cases where using a base temperature of -7 °C improved R^2 values by at least 0.10 over the traditional base temperature of 0 °C. In other cases, a higher base temperature provided a noticeable increase in R^2 value. For example, shifting the base temperature from -7 °C to 2 °C yielded a 25% improvement in R^2 value for inflorescence height in *Poa arctica* at the Barrow Dry site (Fig. 11). Future studies could compare actual tissue temperatures to conditions at canopy height (10 cm) during different light and wind regimes allowing researchers to more accurately assess the true conditions experienced by plants and ultimately improve trait predictability. Future work could also look at the role of freezing degree days in plant phenology as it has been demonstrated that some tundra plant species rely on cooling events to time flowering (Iler & Inouye 2013; Wheeler et al. 2015).

TRACKING ABIOTIC CONDITIONS OVER MULTIPLE YEARS IMPROVED MODELS OF PLANT TRAITS DURING THE CURRENT YEAR

At our sites, leaf length, inflorescence height, and reproductive phenology were more often predicted by factors from the current year while reproductive effort was more often predicted using factors from the previous year (Fig. 8). Reproductive effort responses may be more constrained by abiotic factors during the previous year than those experienced during the current year (Sørensen 1941; Bliss 1971; Meloche & Diggle 2001). Sexual reproduction represents an enormous caloric investment compared to vegetative reproduction (Chapin et al. 1980) and due to the short duration of the growing season in the Arctic, plants must prepare and initiate their flowers during previous seasons in order to ensure pollination and seed set in a following summer (Sørensen 1941). The fact that reproductive efforts in our species could be predicted using conditions during the current year, previous year, or both is likely reflecting this process. For instance: *Cassiope tetragona* is known to increase vegetative growth during favorable growing conditions and then utilize those resources during the consecutive year(s) for reproduction (Johnstone & Henry 1997). Correspondingly, leaf lengths for *C. tetragona* were able to be predicted using abiotic factors during the current year while reproductive efforts could be predicted using those during the previous year. Another illustrative example comes from *Dupontia fisheri*, whose inflorescences are largely self-sustaining, relying fairly little on carbohydrates stored in rhizomes for inflorescence production and growth (Chapin et al. 1980). Correspondingly, abiotic factors during the current year could be used to predict its inflorescence height, whereas those experienced during the previous year could not. Our findings regarding *C. tetragona* and *D. fisheri* indicate that the physiological behaviors of each plant species is an important factor to consider when predicting the impacts of climate change on arctic plants. Considering that many tundra plant species initiate tissue growth two or more years before the plant uses the organs (Meloche & Diggle 2001), it is likely that integrating abiotic factors over a number of years will increase predictability.

SEVERAL SPECIES APPEAR TO BE CAPABLE OF RESPONDING TO CLIMATE CHANGE AT OUR SITES

Our results suggest climate change in the Barrow area will cause shifts in local plant traits and that such processes are likely to persist as the area continues to warm. While we recognize that significant correlations between abiotic factors and plant traits are insufficient to confirm causal linkages, we do have strong evidence that this is the case for at least six of the species we studied as their responses to experimental warming at the same study sites yielded congruent results (Barrett and Hollister, in press; Table 4). Interestingly, two of the species with traits that may be responding to climate change (*Cassiope tetragona* and *Poa arctica*) also showed an increase in percent cover in these sites under experimental warming conditions (Hollister et al. 2005b; Hollister et al. 2015). Future work could help determine whether the plant traits we monitored in this study help explain why their presence in the community has increased (Cleland et al. 2012).

MAKING PLANTS MORE PREDICTABLE: FUTURE WORK

While earlier studies looked for evidence that arctic plant responses to climate change could be generalized to growth form (Arft et al. 1999; Dormann & Woodin 2002), others have confirmed there is a great deal of variability when it comes to predicting how warming will affect a species (Hollister et al. 2005a; Elmendorf et al. 2012b; Høye 2014). This may, in part, be explained by niche differentiation. For example, previous studies have demonstrated that tundra plants avoid interspecific competition by partitioning the rooting depth and timing of nutrient uptake (McKane et al. 2002; Pornon et al. 2007), suggesting that further work to understand the habits of these species may lead to valuable methods for making their responses to climate change more predictable (Kattge et al. 2011; Soudzilovskaia et al. 2013).

While our study focused almost exclusively on the interactions of abiotic factors with individual plant species, further work must integrate biotic and abiotic factors if we want to gain a better understanding of how the Arctic will function under a changing climate. For instance, Becklin et al. (2011) recently demonstrated that climate change impacts arctic plants through multi-level trophic interactions. Additionally, Lamb (2011) showed that ecosystem interactions in the Arctic can be altered through poorly-understood mechanisms as soil microbe communities respond to environmental shifts differently than plants. Furthermore, the addition of other abiotic factors (e.g. PAR, nitrogen availability) may enable a better understanding of how arctic plants respond to climate change.

Ours is one of few long-term plot-level studies that has examined plant response to a wide array of changing abiotic factors. We found that responses are complex, however we do show compelling evidence that climate change is likely to drive change in the growth and reproduction of plants in the Arctic. Recent studies have found increasing plant biomass at several sites since the early 1980's (Hudson et al. 2011; Elmendorf et al. 2012a) and there are several studies showing changes in phenology (Høye et al. 2007; Zeng et al. 2011; Oberbauer et al. 2013). These results are largely consistent with previous predictions that warming will increase plant reproduction and vigor (Arft et al. 1999; Hollister et al. 2005a). The changes we observed are likely to continue as the Arctic continues to warm. Future research should include more long-term studies and examination of multiple biotic and abiotic factors to obtain a clearer picture of how sites are changing over time and how this may be affecting tundra plant species.

Table 4 Species likely to respond to climate change in the Barrow Area. The species presented showed changes in traits that were significantly explained by air temperature using linear mixed models (LMM's) with air degree days as fixed effects and plot and year as random effects. Significant models were identified using a chi-squared likelihood ratio test with and without air degree days as an explanatory variable. Values were then subjected to a Benjamini-Hochberg procedure with a 5% false discovery rate (see Methods section). Additionally, species were only included in this table if they also showed significant responses to a treatment of experimental warming at the same study sites as detailed in Barrett & Hollister (in press). Here we present the effect sizes (Hedges' d) of the significant warming responses from that study in comparison to the marginal R^2 values determined through the LMM's presented in this study. Positive effect sizes signify increased inflorescence height, increased reproductive effort or delayed reproductive phenology.

Trait & Site	Species	Effect size (Hedges' d)	LMM Marginal R^2
Inflorescence height			
Barrow Dry			
	Luzula confusa	1.00	0.15
	Poa arctica	1.33	0.29
	Potentilla hyparctica	1.65	0.30
Reproductive effort			
Barrow Dry			
	Cassiope tetragona	0.84	0.53*
	Poa arctica	0.37	0.25*
Reproductive phenology			
Barrow Dry			
	Cassiope tetragona	-6.30	0.55
	Luzula confusa	-2.39	0.46
	Papaver hultenii	-5.62	0.58
	Poa arctica	-2.32	0.60
	Potentilla hyparctica	-7.55	0.44
Barrow Wet			
	Luzula arctica	-2.17	0.45

*R^2 corresponds to LMM using degree days during previous year

CHAPTER IV: CONCLUSIONS

The results of our work indicate that the growth and reproduction of many arctic plant species are still limited by growing season temperatures despite suggestions of earlier experimental field studies which predicted that such responses would dampen after short-term exposure to warming. In contrast, this study supports the idea that inter-annual variability and other factors will buffer arctic species from experiencing a resource burn-out, effectively allowing them to sustain their responses to climate change in the Arctic over a multi-decadal time scale. However, our results also illustrate that such responses will not continue indefinitely as we revealed that experimental warming may already be having less effect on reproductive phenology as the region has warmed in recent years. It is likely and that this will happen with other plant traits as well. Our study also shows that many abiotic factors influence plant performance in addition to air temperature and that arctic plant responses to warming vary greatly by species and site. However, we have demonstrated that continuously monitoring air and soil temperatures as well as other abiotic factors can provide valuable predictive power when it comes to forecasting how plant traits will respond to climate change. This is especially true for reproductive effort which is greatly affected by conditions during the years leading up to flower burst. The fact that multiple species showed significant changes over time at these study sites while few of the abiotic factors did speaks both to the fact that more work is needed to understand how and why arctic plants respond to climate change and to the idea that studies are unlikely to be successful in predicting these relationships without a broad range of measures when it comes to abiotic and biotic factors in the area.

It is clear that tundra plants at these study sites are responsive to changes in temperature and capable of maintaining their responses over multi-decadal periods of time. However, future research is needed in order to ascertain how the trait-level responses of individual species will alter energy balance, trophic interactions, and community compositions. One such study could focus on changes in community structure at these study sites and compare shifts in abundance and diversity with the findings of this study to elucidate potential drivers for changes in community composition. Such relationships could provide invaluable clues in predicting how the Arctic will continue responding to climate change.

REFERENCES

ACIA. 2005. Impacts of a warming arctic: Arctic climate impact assessment. Cambridge: Cambridge University Press.

Aerts R. 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology* 94, 713-724.

Åkerman H.J. & Johansson M. 2008. Thawing permafrost and thicker active layers in sub-arctic Sweden. *Permafrost and Periglacial Processes* 19: 279-292.

Arft A.M., Walker M.D., Gurevitch J., Alatalo J.M., Bret-Harte M.S., Dale M.R.T., Diemer M.C., Gugerli F., Henry G.H.R., Jones M.H., Hollister R.D., Jónsdóttir I.S., Laine K., Lévesque E., Marion G.M., Molau U., Mølgaard P., Nordenhall U., Raszhivin V., Robinson C.H., Starr G., Stenström A., Stenström M., Totland Ø., Turner P.L., Walker L.J., Webber P.J., Welker J.M. & Wookey P.A. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. Ecological Monographs 64, 491-511.

Barrett, R. T. & R. D. Hollister. In press. Arctic plants are capable of sustained responses to long-term warming. *Polar Research*.

Bates D., Maechler M., Bolker B. & Walker S. 2015. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-8, <URL: http://CRAN.R-project.org/package=lme4>

Batzli G. O. 1980. Research on Arctic Tundra Environments (RATE) program. *Special issue of Arctic and Alpine Research. Arctic and Alpine Research* 12, 4.

Becklin K. M., Gamez G., Uelk B., Raguso R. A. & Galen C. 2011. Soil fungal effects on floral signals, rewards, and aboveground interactions in an Alpine pollination web. *American Journal of Botany* 98: 1299-1308.

Bennington C.C., Fetcher N., Vavrek M.C., Shaver G.R., Cummings K.J. & McGraw J.B. 2012. Home site advantage in two long-lived arctic plant species: Results from two 30-year reciprocal transplant studies. *Journal of Ecology* 100, 841-851.

Billings W.D. & Mooney H.A. 1968. The ecology of arctic and alpine plants. *Biological Review* 43, 481-529.

Bliss, L. C. 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics* 2: 405-438.

Bliss L. C., Courtin G. M., Pattie D. L., Riewe R. R., Whitfield D. W. A. & Widden P. 1973. Arctic tundra ecosystems. *Annual Review of Ecology and Systematics* 4: 359-399.

Boelman N.T., Stieglitz M., Rueth H.M., Sommerkorn M., Griffin K.L., Shaver G.R. & Gamon J.A. 2003. Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia* 135, 414-421.

Bokhorst S., Bjerke J.W., Bowles F.W., Melillo J., Callaghan T.V. & Phoenix G.K. 2008. Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. *Global Change Biology*, 14, 2603-2612.

Brown J., Everett K. R., Webber P. J., Maclean S. F., & Murray D. F. 1980. The coastal tundra at Barrow. In Brown J., Miller P. C., Tieszen L. L. & Bunnell F. L. [eds.], An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska. 1-29. Dowden, Hutchinson, & Ross, Inc., Stroudsburg, Pennsylvania, USA.

Callaghan, T. V., Carlsson B. Å. & Tyler N. J. C. 1989. Historical records of climate-related growth in *Cassiope tetragona* from the Arctic. Journal of Ecology 77: 823-837.

Campioli M., Schmidt N.M., Albert K.R., Leblans N., Ro-Poulsen H. & Michelsen A. 2013. Does warming affect growth rate and biomass production of shrubs in the High Arctic? Plant Ecology 214, 1049-1058.

Chapin F.S. III & Chapin M.C. 1981. Ecotypic differentiation of growth processes in *Carex aquatilis* along latitudinal and local gradients. Ecology 62, 1000-1009.

Chapin F.S., III, McGuire A.D., Randerson J., Pielke R., Baldocchi D., Hobbie S.E., Roulet N., Eugster W., Kasischke E., Rastetter E.B., Zimov S.A. & Running S.W. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology* 6, 211-223.

Chapin F.S. III & Shaver G.R. 1985a. Arctic. In: Physiological Ecology of North American Plant Communities (eds Chabot B. & Mooney H.), pp. 16-40. Chapman and Hall, New York.

Chapin F.S. III & Shaver .G.R. 1985b. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66, 564-576.

Chapin F.S. III, Shaver G.R., Giblin A.E., Nadelhoffer K.J. & Laundre J.A. 1995. Response of arctic tundra to experimental and observed changes in climate. Ecology 76, 696-711.

Chapin F.S. III, Sturm M., Serreze M.C., McFadden J.P., Key J.R., Lloyd A.H., McGuire A.D., Rupp T.S., Lynch A.H., Schimel J.P., Beringer J., Chapman W.L., Epstein H.E., Euskirchen E.S., Hinzman L.D., Jia G., Ping C.L., Tape K.D., Thompson C.D.C., Walker D.A. & Welker J.M. 2005. Role of land-surface changes in arctic summer warming. Science 310, 657-660.

Chapin F. S. III, Tieszen L. L., Lewis M. C., Miller P. C. & McCown B. H.1980. Control of tundra plant allocation patters and growth. In J. Brown, P. C. Miller, L. L. Tieszen, and F. L. Bunnell [eds.], An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska 140-185. Dowden, Hutchinson, & Ross, Inc., Stroudsburg, Pennsylvania, USA.

Cleland E. E., Allen J. M., Crimmins T. M., Dunne J. A., Pau S., Travers S. E., Zavaleta E. S. & Wolkovich E. M. 2012. Phenological tracking enables positive species responses to climate change. Ecology 93: 1765-1771.

Dorji T., Totland Ø., Moe S.R., Hopping K.A., Pan J.B. & Klein J.A. 2013. Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. Global Change Biology 19, 459-472.

Dormann C.F. & Woodin S.J. 2002. Climate change in the Arctic: Using plant functional types in a meta-analysis of field experiments. Functional Ecology 16, 4-17.

Dunne J.A., Harte J. & Taylor K.J. 2003. Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. Ecological Monographs 73, 69-86.

Elmendorf S. C., Henry G. H. R., Hollister R. D., Björk R. G., Boulanger-Lapointe N., Cooper E. J., Cornelissen, J.H.C., Day, T.A., Dorrepaal, E., Elumeeva, T.G., Gill, M., Gould, W.A., Harte, J., Hik, D.S., Hofgaard, A., Johnson, D.R., Johnstone, J.F., Jonsdottir, I.S., Jorgenson, J.C., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lara, M., Levesque, E., Magnusson, B., May, J.L., Mercado-Diaz, J.A., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Onipchenko, V.G., Rixen, C., Schmidt, N.M., Shaver, G.R., Spasojevic, M.J., Thorhallsdottir, Th.E., Tolvanen, A., Troxler, T., Tweedie, C.E., Villareal, S., Wahren,C.-H., Walker, X., Webber, P.J., Welker, J.M., Wipf, S. 2012a.

Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nature Climate Change 2: 453-457.

Elmendorf S.C., Henry G.H.R., Hollister R.D., Bjork R.G., Bjorkman A.D., Callaghan T.V., Collier L.S., Cooper E.J., Cornelissen J.H.C., Day T.A., Fosaa A.M., Gould W.A., Grétarsdóttir J., Harte J., Hermanutz L., Hik D.S., Hofgaard A., Jarrad F., Jónsdóttir I.S., Keuper F., Klanderud K., Klein J.A., Koh S., Kudo G., Lang S.I., Loewen V., May J.L., Mercado J., Michelsen A., Molau U., Myers-Smith I.H., Oberbauer S.F., Pieper S., Post E., Rixen C., Robinson C.H., Schmidt N.M., Shaver G.R., Stenström A., Tolvanen A., Totland Ø., Troxler T., Wahren C.H., Webber P.J., Welker J.M. & Wookey P.A. 2012b. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. Ecology Letters 15, 164-175.

Euskirchen E. S., Mcguire A. D. & Chapin F. S. III. 2007. Energy feedbacks of northern high-latitude ecosystems to the climate system due to reduced snow cover during 20th century warming. Global Change Biology 13: 2425-2438.

Fraser L. H., Henry H.A.L., Carlyle C. N., White S. R., Beierkuhnlein C., Cahill J. F., Casper B. B., Cleland E., Collins S. L., Dukes J. S., Knapp A. K., Lind E., Long R. J., Luo Y. Q., Reich P. B., Smith M. D., Sternberg M. & Turkington R. 2013. Coordinated distributed experiments: An emerging tool for testing global hypotheses in ecology and environmental science. Frontiers in Ecology and the Environment 11: 147-155.

Gauthier G., Bety J., Cadieux M.C., Legagneux P., Doiron M., Chevallier C., Lai S., Tarroux A. & Berteaux D. 2013. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra.

Philosophical Transactions of the Royal Society B-Biological Sciences 368, 20120482 1-12.

Gilg O., Sittler B. & Hanski I. 2009. Climate change and cyclic predator-prey population dynamics in the High Arctic. Global Change Biology 15, 2634-2652.

Gugerli F. & Bauert M.R. 2001. Growth and reproduction of Polygonum viviparum show weak responses to experimentally increased temperature at a Swiss Alpine site. Botanica Helvetica 111, 169-180.

Hedenås H., Carlsson B.Å., Emanuelsson U., Headley A.D., Jonasson C., Svensson B.M. & Callaghan T.V. 2012. Changes versus homeostasis in alpine and sub-alpine vegetation over three decades in the sub-arctic. Ambio 41, 187-196.

Hinkel K. M. & F. E. Nelson. 2003. Spatial and temporal patterns of active layer thickness at Circumpolar Active Layer Monitoring (CALM) sites in northern Alaska, 1995-2000. Journal of Geophysical Research-Atmospheres 108: 8168 1-13.

Hinzman, L. D., Bettez N., Chapin F. S. III, Dyurgerov M., Fastie C. L., Griffith B., Hollister R. D., Hope A., Huntington H. P., Jensen A., Kane D. L., Klein D. R., Lynch A. H., Lloyd A., Mcguire D., Nelson F. E., Oechel W. C., Osterkamp T. E., Racine C., Romanovsky V. E., Stow D., Sturm M., Tweedie C. E., Vourlitis G., Walker M. D., Walker D. A., Webber P. J., Welker, J. M., Winker K. & Yoshikawa K. 2005. Evidence and implications of recent climate change in terrestrial regions of the Arctic. Climatic Change 72: 251-298.

Hoffmann A. A., Camac J. S., Williams R. J., Papst W., Jarrad F. C. & Wahren C. H. 2010. Phenological changes in six Australian subalpine plants in response to experimental warming and year-to-year variation. Journal of Ecology 98: 927-937.

Hollister R.D. 2003. Response of tundra vegetation to temperature: Implications for forecasting vegetation change. PhD Thesis, Michigan State University.

Hollister R.D., Webber P.J. & Tweedie C.E. 2005a. The response of Alaskan arctic tundra to experimental warming: Differences between short- and long-term responses. Global Change Biology 11, 525-536.

Hollister R.D., Webber P.J. & Bay C. 2005b. Plant response to temperature in northern Alaska: Implications for predicting vegetation change. Ecology 86, 1562-1570.

Hollister R. D., May J. L., Kremers K. S., Tweedie C. E., Oberbauer S. F., Liebig J. A., Botting T. F., Barrett R. T. &. Gregory J. L. 2015. Warming experiments elucidate the drivers of observed directional changes in tundra vegetation. Ecology and Evolution 5: 1881-1895.

Hollister R.D., Webber P.J., Nelson F.E. & Tweedie C.E. 2006. Soil thaw and temperature response to air warming varies by plant community: Results from an open-top chamber experiment in northern Alaska. Arctic Antarctic and Alpine Research 38, 206-215.

Hollister R.D., Webber P.J., Slider R.T., Nelson F.E. & Tweedie C.E. 2008. Soil temperature and thaw response to manipulated air temperature and plant cover at Barrow and Atqasuk, Alaska. In D.L. Kane & K.M. Hinkel (eds.) Ninth International Conference on Permafrost. Pp. 729-734. Fairbanks: Institute of Northern Engineering.

Høye T. T. 2014. Reducing uncertainty in species' responses to climate change. Current Zoology 60: 186-188.

Hudson J.M.G. & Henry G.H.R. 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology 90, 2657-2663.

Hudson J.M.G., Henry G.H.R. & Cornwell W.K. 2011. Taller and larger: Shifts in arctic tundra leaf traits after 16 years of experimental warming. Global Change Biology 17, 1013-1021.

Iler A.M. & Inouye D.W. 2013. Effects of climate change on mast-flowering cues in a clonal montane herb, *Veratrum tenuipetalum* (Melanthiaceae). American Journal of Botany 100, 519-525.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.

Johnstone, J. & Henry G. H. R. 1997. Retrospective analysis of growth and reproduction in Cassiope tetragona and relations to climate in the Canadian High Arctic. Arctic and Alpine Research 4: 459-469.

Jorgenson M. T., Shur Y. L. & Pullman E. R. 2006. Abrupt increase in permafrost degradation in Arctic Alaska. Geophysical Research Letters 33: L02503 1-4.

Kattge J., Díaz S., Lavorel S., Prentice C., Leadley P., Bönisch G., Garnier E., Westoby M., Reich P. B., Wright I. J., Cornelissen J. H. C., Violle C., Harrison S. P., Van Bodegom P. M., Reichstein M., Enquist B. J., Soudzilovskaia N. A., Ackerly D. D., Anand M., Atkin O., Bahn M., Baker T. R., Baldocchi D., Bekker R., Blanco C. C., Blonder B., Bond W. J., Bradstock R., Bunker D. E., Casanoves F., Cavender-Bares J., Chambers J. Q., Chapin F. S. III, Chave J., Coomes D., Cornwell W. K., Craine J. M., Dobrin B. H., Duarte L., Durka W., Elser J., Esser G., Estiarte M., Fagan W. F., Fang J., Fernández-Méndez F., Fidelis A., Finegan B., Flores O., Ford H., Frank D., Freschet G. T., Fyllas N. M., Gallagher R. V., Green W. A., Gutierrez A.G., Hickler T., Higgins S. I., Hodgson J. G., Jalili A., Jansen S., Joly C. A., Kerkhoff A. J., Kirkup D., Kitajima K., Kleyer M., Klotz S., Knops J. M. H., Kramer K., Kühn I., Kurokawa H., Laughlin D., Lee T. D., Leishman M., Lens F., Lenz T., Lewis S. L., Lloyd J., Llusià J., Louault F., Ma S., Mahecha1 M. D., Manning P., Massad T., Medlyn B. E., Messier J., Moles A. T., Müller S. C., Nadrowski K., Naeem S., Niinemets Ü., Nöllert S., Nüske A., Ogaya R., Oleksyn J., Onipchenko V. G., Onoda Y., Ordoñez J., Overbeck G., Ozinga W. A., Patiño S., Paula S., Pausas J. G., Peñuelas J., Phillips O. L., Pillar V., Poorter H., Poorter L., Poschlod P., Prinzing A., Proulx R., Rammig A., Reinsch S., Reu1 B., Sack L., Salgado-Negret B., Sardans J., Shiodera S., Shipley B., Siefert A., Sosinski E.,. Soussana J.-F, Swaine E., Swenson N., Thompson K., Thornton P., Waldram M., Weiher E., White M., White S., S. Wright J., Yguel B., Zaehle S., Zanne A. E. & Wirth C. 2011. TRY - a global database of plant traits. Global Change Biology 17: 2905-2935.

Kittel T. G. F., Baker B. B., Higgins J. V. & Haney J. C. 2011. Climate vulnerability of ecosystems and landscapes on Alaska's North Slope. Regional Environmental Change 11: S249-S264.

Klady R.A., Henry G.H.R. & Lemay V. 2011. Changes in high arctic tundra plant reproduction in response to long-term experimental warming. Global Change Biology 17, 1611-1624.

Lamb E. G., Han S., Lanoil B. D., Henry G. H. R., Brummell M. E., Banerjee S. & Siciliano S. D. 2011. A High Arctic soil ecosystem resists long-term environmental manipulations. Global Change Biology 17: 3187-3194.

Lambrecht S.C., Loik M.E., Inouye D.W. & Harte J. 2007. Reproductive and physiological responses to simulated climate warming for four subalpine species. New Phytologist 173, 121-134.

Marchand F.L., Nijs I., Heuer M., Mertens S., Kockelbergh F., Pontailler J-Y., Impens I. & Beyens L. 2004. Climate warming postpones senescence in High Arctic tundra. Arctic Antarctic and Alpine Research, 36, 390-394.

Marion G. M., Henry G. H. R., Freckman D. W., Johnstone J., Jones G., Jones M. H., Lévesque E., Molau U., P. Mølgaard, Parsons A. N., Svoboda J. & Virginia R. A. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biology 3: 20-32.

Mazer S.J., Travers S.E., Cook B.I., Davies T.J., Bolmgren K., Kraft N.J.B., Salamin N. & Inouye D.W. 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.

McKane R. B., Johnson L.C., Shaver G.R., Nadelhoffer K. J., Rastetter E. B., Fry B., Giblin A. E., Kielland K., Kwiatkowski B.L., Laundre J.A. & Murray G. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415: 68-71.

Meloche C. G. & Diggle P. K. 2001. Preformation, architectural complexity, and developmental flexibility in Acomastylis rossii (Rosaceae). American Journal of Botany 88: 980-991.

Michelsen A., Rinnan R. & Jonasson S. 2012. Two decades of experimental manipulations of heaths and forest understory in the subarctic. Ambio 41, 218-230.

Molau U. editor. 1993. International Tundra Experiment (ITEX) Manual. Danish Polar Center, Copenhagen, Denmark.

Molau U., Nordenhall U. & Eriksen B. 2005. Onset of flowering and climate variability in an alpine landscape: A 10-year study from Swedish Lapland. American Journal of Botany 92: 422-431.

Natali S.M., Schuur E.A.G. & Rubin R.L. 2012. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. Journal of Ecology 100, 488-498.

Oberbauer S.F., Elmendorf S.C., Troxler T.G., Hollister R.D., Rocha A.V., Bret-Harte M.S., Dawes M.A., Fosaa A.M., Henry G.H.R., Høye T.T., Jarrad F.C., Jónsdóttir I.S., Klanderud K., Klein J.A., Molau U., Rixen C., Schmidt N.M., Shaver G.R., Slider R.T., Totland Ø., Wahren C.-H. & Welker J.M. 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. Philosophical Transactions of the Royal Society B-Biological Sciences 368, 1-13.

Oberbauer S.F., Tweedie C.E., Welker J.M., Fahnestock J.T., Henry G.H.R., Webber P.J., Hollister R.D., Walker M.D., Kuchy A., Elmore E. & Starr G. 2007. Tundra CO2 fluxes in response to experimental warming across latitudinal and moisture gradients. Ecological Monographs 77, 221-238.

Park H., Yabuki H. & Ohata T. 2012. Analysis of satellite and model datasets for variability and trends in Arctic snow extent and depth, 1948-2006. Polar Science 6: 23-37.

Penuelas J., Rutishauser T. & Filella I. 2009. Phenology Feedbacks on Climate Change. Science, 324, 887-888.

Pornon A., Escaravage N. & Lamaze T. 2007. Complementarity in mineral nitrogen use among dominant plant species in a subalpine community. American Journal of Botany 94: 1778-1785.

Post E. & Forchhammer M.C. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B-Biological Sciences 363, 2369-2375.

Post E., Forchhammer M. C., Bret-Harte M. S., Callaghan T. V., Christensen T. R., Elberling B., Fox A. D., Gilg O., Hik D.S., Høye T.T., Ims R.A., Jeppesen E., Klein D.R., Madsen J., McGuire A.D., Rysgaard S., Schindler D.E., Stirling I., Tamstorf M.P., Tyler N.J.C., van der Wal R., Welker J., Wookey P.A., Schmidt N.M. & Aastrup P. 2009. Ecological dynamics across the Arctic associated with recent Climate Change. Science 325: 1355-1358.

Post E., Pedersen C., Wilmers C.C. & Forchhammer M.C. 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. Proceedings of the Royal Society B-Biological Sciences 275, 2005-2013.

Press M. C., Potter J. A., Burke M. J. W., Callaghan T. V. & Lee J. A. 1998. Responses of a subarctic dwarf shrub heath community to simulated environmental change. Journal of Ecology 86: 315-327.

R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Rosenberg M.S., Adams D.C. & Gurevitch J. 2000. Metawin: Statistical Software for Meta-Analysis with Resampling Tests. Version 2.0. Sinauer Associates. Sunderland, Massachusetts, USA.

Savile, D. B. O. 1972. Arctic adaptations in plants. Canadian Department of Agriculture Monograph 6: 1-81.

Serreze M. C., Walsh J. E., Chapin F.S. III, Osterkamp T. E., Dyurgerov M., Romanovsky V. E., Oechel W.C., Morison J., Zhang T. & Barry R.G. 2000. Observational evidence of recent change in the northern high-latitude environment. Climatic Change 46: 159-207.

Shaver G.R. & Jonasson S. 1999. Response of arctic ecosystems to climate change: Results of long-term field experiments in Sweden and Alaska. Polar Research 18, 245-252.

Shaver, G. R. & Kummerow J. 1992. Phenology, resource allocation, and growth of arctic vascular plants. In Chapin F.S. III, Jefferies R.L., Reynolds J.F., Shaver G.R. & Svoboda J. (eds.) Arctic Ecosystems in a Changing Climate An Ecophysiological Perspective. Pp. 193-211. San Diego: Academic Press.

Sherry R.A., Zhou X.H., Gu S.L., Arnone J.A. III, Schimel D.S., Verburg P.S., Wallace L.L., & Luo Y. 2007. Divergence of reproductive phenology under climate warming. Proceedings of the National Academy of Sciences of the United States of America, 104, 198-202.

Shiklomanov N. I., Streletskiy D. A., Nelson F. E., Hollister R. D., Romanovsky V. E., Tweedie C. E., Bockheim J. G. & Brown J. 2010. Decadal variations of active-layer thickness in moisture-controlled landscapes, Barrow, Alaska. Journal of Geophysical Research-Biogeosciences 115: G00104 1-14.

Sørensen T. 1941. Temperature relations and phenology of northeast Greenland flowering plants. Meddelelser om Grønland 125: 1-305.

Soudzilovskaia N. A., Elumeeva T. G., Onipchenko V. G., Shidakov I. I., Salpagarova F. S., Khubiev A. B., Tekeev D. K. & Cornelissen J. H. C. 2013. Functional traits predict relationship between plant abundance dynamic and long-term climate warming. Proceedings of the National Academy of Sciences of the USA 110: 18180-18184.

Starr G., Oberbauer S.F. & Pop E.W. 2000. Effects of lengthened growing season and soil warming on the phenology and physiology of Polygonum bistorta. Global Change Biology, 6, 357-369.

Stenström A., Jónsdóttir I. S. & Augner M. 2002. Genetic and environmental effects on morphology in clonal sedges in the Eurasian Arctic. American Journal of Botany 89: 1410-1421.

Stone R. S., Dutton E. G., Harris J. M. & Longenecker D. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change. Journal of Geophysical Research-Atmospheres 107: D10 1-15.

Stow D. A., Hope A., McGuire D., Verbyla D., Gamon J., Huemmrich F., Houston S., Racinef C., Sturm M., Tape K, Hinzman L., Yoshikawai K., Tweedie C.E., Noylek B., Silapaswanl C., Douglas D., Griffith B., Jiao G., Epstein H., Walker D.A., Daeschner S., Petersen A., Zhou L. & Mynenir R. 2004. Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. Remote Sensing of Environment 89: 281-308.

Tape K., Sturm M. & Racine C. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12: 686-702.

Thórhallsdóttir T.E. 1998. Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. Oecologia 114, 43-49.

Verbyla D. 2008. The greening and browning of Alaska based on 1982-2003 satellite data. Global Ecology and Biogeography 17: 547-555.

Walker M.D., Wahren C.H., Hollister R.D., Ahlquist L.E., Alatalo J.M, Bret-Harte S.M, Calef M.P., Callaghan T.V. & Carroll A.B. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America, 103, 1342-1346.

Walker M. D., Webber P. J., Arnold E. H. & Ebert-May D. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. Ecology 75: 393-408.

Wendler G., Moore B. & Galloway K. 2014. Strong temperature increase and shrinking sea ice in Arctic Alaska. The Open Atmospheric Science Journal 8: 7-15.

Wheeler H. C., Høye T. T., Schmidt N. M., Svenning J-C. & Forchhammer M. C. 2015. Phenological mismatch with abiotic conditions-implications for flowering in Arctic plants. Ecology 96: 775-787.

Zeng H.Q., Jia G. S. & Epstein H. 2011. Recent changes in phenology over the northern high latitudes detected from multi-satellite data. Environmental Research Letters 6: 045508 1-11.