

Arctic plant responses to changing abiotic factors in northern Alaska¹

Robert T. S. Barrett^{2,3,6}, Robert D. Hollister², Steven F. Oberbauer⁴, and Craig E. Tweedie⁵

PREMISE OF THE STUDY: Understanding the relationship between plants and changing abiotic factors is necessary to document and anticipate the impacts of climate change.

METHODS: We used data from long-term research sites at Barrow and Atkasuk, Alaska, to investigate trends in abiotic factors (snow melt and freeze-up dates, air and soil temperature, thaw depth, and soil moisture) and their relationships with plant traits (inflorescence height, leaf length, reproductive effort, and reproductive phenology) over time.

KEY RESULTS: Several abiotic factors, including increasing air and soil temperatures, earlier snowmelt, delayed freeze-up, drier soils, and increasing thaw depths, showed nonsignificant tendencies over time that were consistent with the regional warming pattern observed in the Barrow area. Over the same period, plants showed consistent, although typically nonsignificant tendencies toward increasing inflorescence heights and reproductive efforts. Air and soil temperatures, measured as degree days, were consistently correlated with plant growth and reproductive effort. Reproductive effort was best predicted using abiotic conditions from the previous year. We also found that varying the base temperature used to calculate degree days changed the number of significant relationships between temperature and the trait: in general, reproductive phenologies in colder sites were better predicted using lower base temperatures, but the opposite held for those in warmer sites.

CONCLUSIONS: Plant response to changing abiotic factors is complex and varies by species, site, and trait; however, for six plant species, we have strong evidence that climate change will cause significant shifts in their growth and reproductive effort as the region continues to warm.

KEY WORDS abiotic factors; climate change; ITEX; LMM; northern Alaska; phenology; tundra plants

Climate change is impacting terrestrial ecosystems worldwide, and the Arctic has been warming faster and with greater magnitude than other regions (ACIA, 2005; IPCC, 2013). Recent changes in the Arctic include earlier snowmelts, longer growing seasons, warmer temperatures, and increasing thaw depths (ACIA, 2005). Tundra vegetation has begun responding to these shifts through altered plant growth and phenology, northward expansion of shrubs

and trees, and altered community compositions (ACIA, 2005; 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 and 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 1980s, 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, warmer soils, increased nutrient availability,

¹ Manuscript received 6 December 2014; revision accepted 5 November 2015.

² Biology Department, Grand Valley State University, 1 Campus Drive, Allendale, Michigan 49401 USA;

³ West Michigan Academy of Environmental Science, 4463 Leonard Street, Walker, Michigan 49534 USA;

⁴ Department of Biological Sciences, Florida International University 11200 SW 8th Street, Miami, Florida 33199 USA; and

⁵ Department of Biology, University of Texas at El Paso, El Paso, Texas 79968 USA

⁶ Author for correspondence (e-mail: robertbarrett@choiceschools.com), phone 517-896-6194

doi:10.3732/ajb.1400535

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 and 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?

MATERIALS AND METHODS

Study sites—This study took place at field sites near Barrow (71°18'N, 156°40'W) and Atqasuk (70°29'N, 157°25'W), Alaska, United States. 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 to 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 m²), half of which were experimentally warmed using Open Top Chambers (OTCs, 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 to compare our results in this study with those presented in a separate study at the same sites (Barrett and 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 by Hollister et al. (2005a, b). Both locations have a deep heritage of research; Barrow was an International Biological Tundra Biome site in the early 1970s (Brown et al., 1980), and Atqasuk was the focus of the Research on Arctic Tundra Environments (Batzli, 1980).

Abiotic factors—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 [R. D. Hollister, unpublished data].) Freeze-up date was defined as the day of year soil temperatures at 10 cm depth dropped and remained below 0°C. 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, Virginia, USA). 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 Corp., Pocasset, Massachusetts, USA; Model 107 Temperature Probe, Campbell Scientific, Logan, Utah, USA; and MRC TP101M Temperature Probes, Measurement Research Corp., Gig Harbor, Washington, USA). During the 1999–2001 field seasons, early season air temperatures were missing from snowmelt until loggers were placed (up to 9 d after snowmelt but typically fewer than 5 d). These missing temperatures were estimated using climate tower readings from the dry sites (Barrett and 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 belowground for the duration of the summer (snowmelt date through 15 August) or fall (15 August 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 traits—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*, for which 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 the length of its most recent annual growth increment (Callaghan et al., 1989; Johnstone and Henry, 1997). For inflorescence height and leaf length, we used maximum size reached by an individual plant during the summer growing period (snowmelt to 15 August). 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. Up to three permanently marked individuals were measured per plot. In many cases, markers were lost between years, and new individuals were randomly chosen. The three largest reproductive individuals within a plot were also measured. 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 (flowering date) 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 10 plots of each treatment type were observed for all plant traits due to logistical constraints.

Statistical analysis—Trends in abiotic factors over time were examined using linear regressions in the program R (R Development Core Team, 2005). To determine whether the traits of individual species had changed over time, we used linear mixed models (LMMs) using a Gaussian error distribution in which we treated year as a fixed effect and plot and year as random effects. These tests were performed using the lme4 package in R (Bates et al., 2015). To determine whether a trait showed a significant trend over time, a χ^2 likelihood ratio test was performed between models with and without time as an explanatory variable ($\alpha = 0.05$) in R (R Development Core Team, 2005). To relate traits of a species to each abiotic factor of interest, we also used LMMs with the abiotic factor of interest as a fixed effect and plot and year as random effects. We then used a χ^2 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 4 years of study; 10 species met this criteria at the AD site, six at the AW site, 14 at the BD site, and 17 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. 1; Appendices S1 and S2, see Supplemental Data with the online version of this article). However, most abiotic factors showed nonsignificant tendencies consistent with a warming Arctic (Fig. 1); these included nonsignificant 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 nonsignificant 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. 2; Appendices S3 and S4, see online Supplemental Data). 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). Two percent of plant species trended toward increasing reproductive efforts over time, while 2% had the opposite trend. 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.

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. 3, online Appendices S5 and S6). 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.

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. However, 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. 4). 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 *Hierochloa 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. 5). 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. 6). 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 Atkasuk 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 Atkasuk showed this relationship. Furthermore, 60% of Atkasuk 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.

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., 2010) 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 nonsignificant, they were all in the same direction (Fig. 1C, F). The growing season length has been increasing through a combination of earlier snowmelt and delayed freeze-up (Fig. 1A, B). These findings are consistent with those of several larger-scale studies using satellite observations, which showed a pattern of increased growing season lengths throughout the Arctic, resulting in greener summers for tundra biomes (Stow

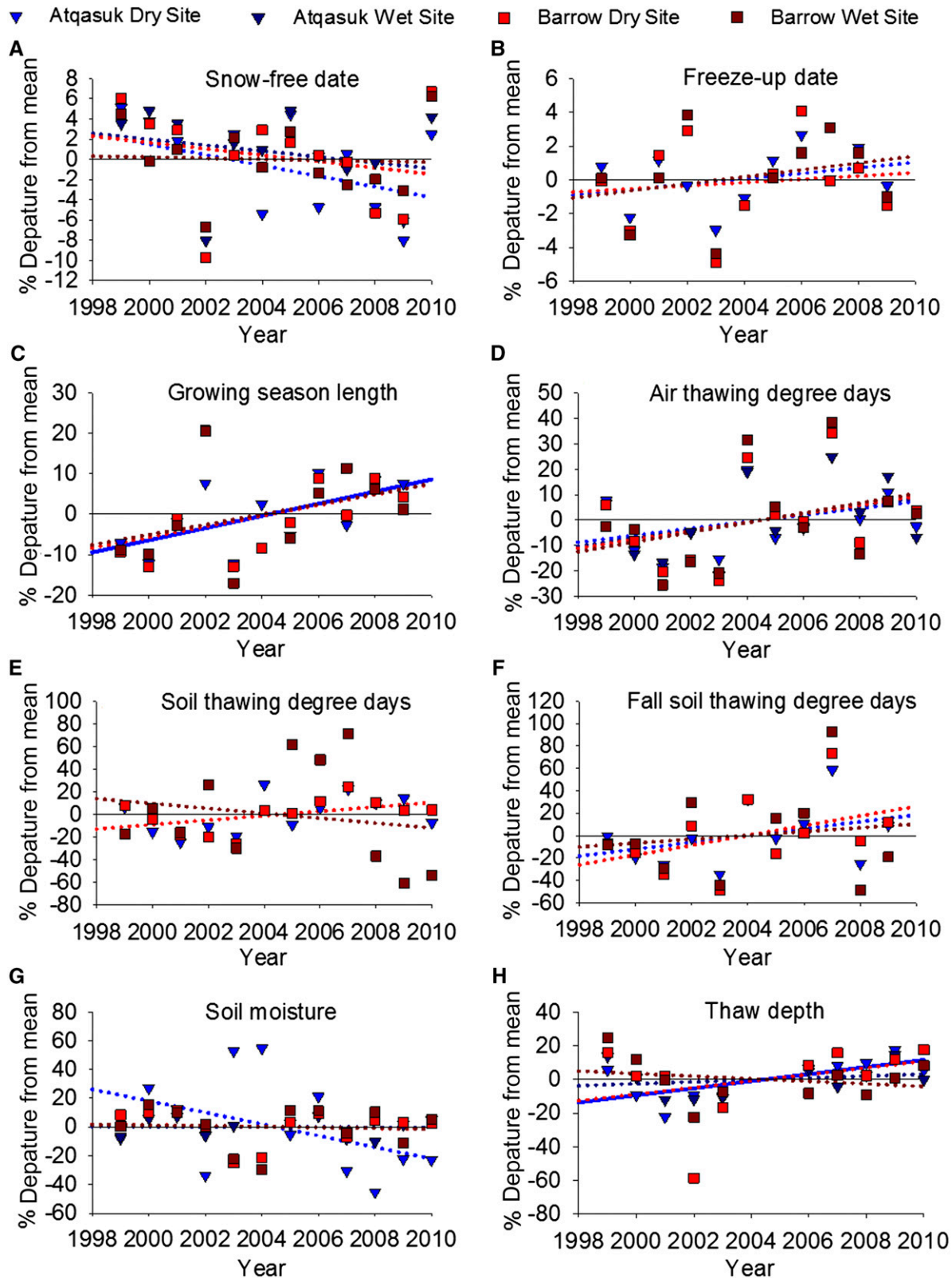


FIGURE 1 Trends in (A) snow free date, (B) freeze-up date, (C) growing season length, (D) air thawing degree days, (E) soil thawing degree days, (F) fall soil thawing degree days, (G) soil moisture, and (H) thaw depth over time at each site. Each point represents the percentage departure each year from the average during the study. Significant trends from linear regressions are shown as solid lines; nonsignificant tendencies are shown as dashed lines. Further details for each abiotic factor are discussed in the Materials and Methods. See Appendix S1 for the mean values of all factors and Appendix S2 for details on each analysis.

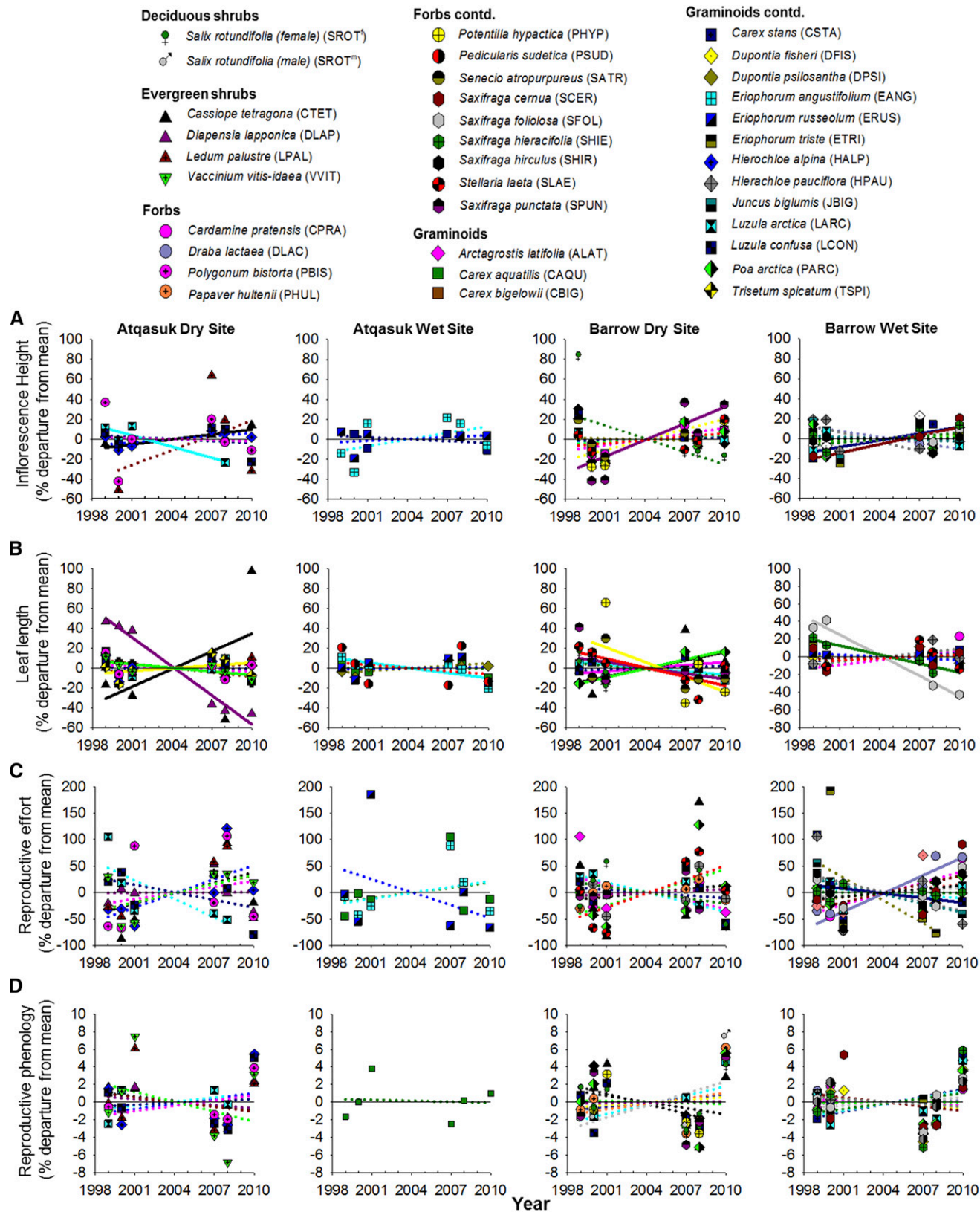


FIGURE 2 Trends in (A) inflorescence height, (B) leaf length, (C) reproductive effort, and (D) reproductive phenology over time for each plant species at each site. Each point represents the percentage departure each year for a species from its average value during the study. Significant trends from a linear mixed model are shown as solid lines; nonsignificant tendencies are shown as dashed lines. Further details for each plant trait and statistical procedures are discussed in the Materials and Methods. See Appendix S3 for the mean values of all plant traits and Appendix S4 for details on each analysis.

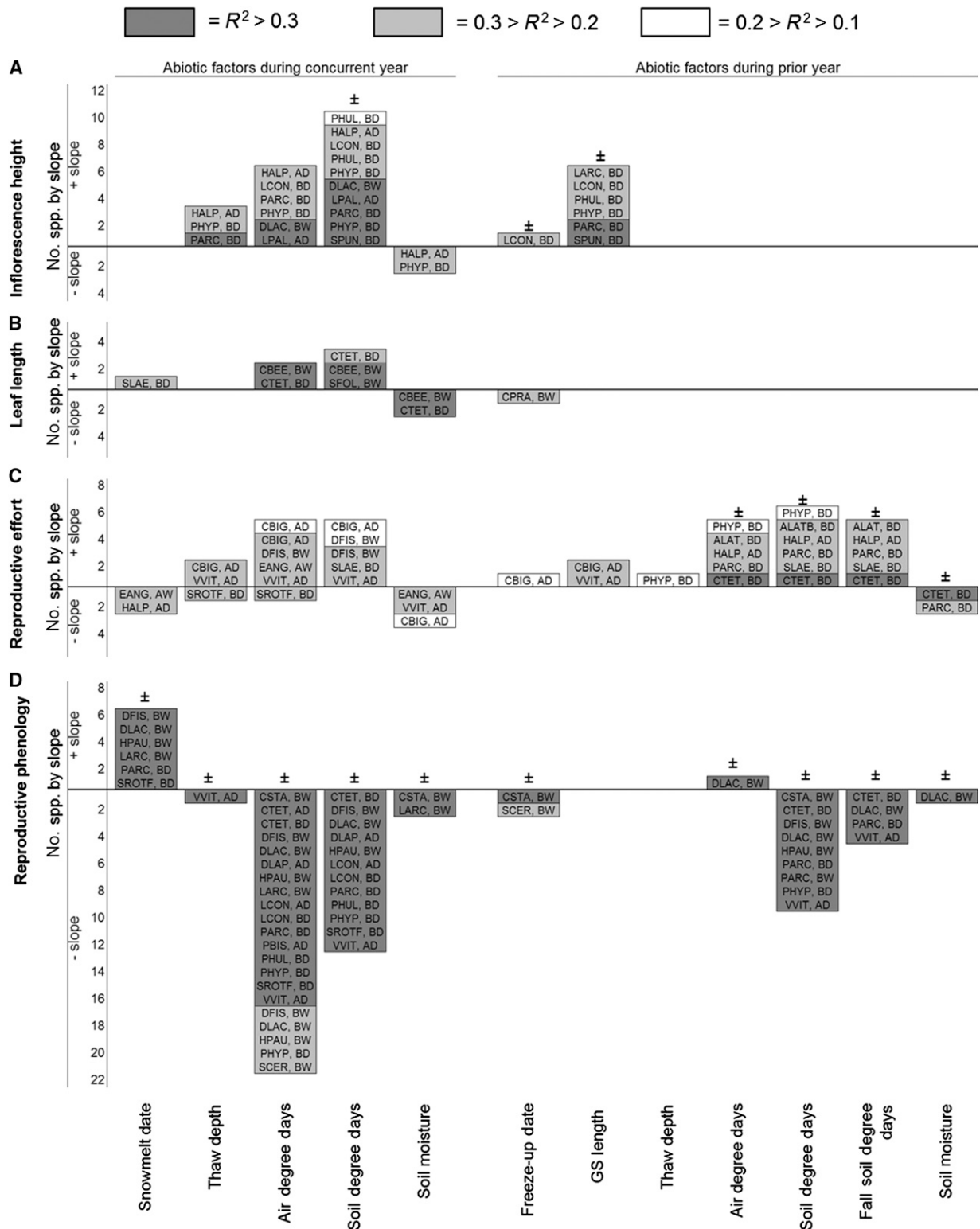


FIGURE 3 Relationships between plant traits and abiotic factors. The following plant traits were included: (A) inflorescence height, (B) leaf length, (C) reproductive effort, and (D) reproductive phenology. Each bar represents a species from a site that showed a significant linear mixed model where abiotic factors were considered fixed effects, while plot and year were treated as random effects. The number of species at a site combinations for which models were run was between 35 and 40 unless denoted (\pm 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 χ^2 likelihood test. For a description of the abiotic factors, see Fig. 1; for species codes, see Fig. 2. Site abbreviations: Atqasuk Dry (AD), Atqasuk Wet (AW), Barrow Dry (BD), and Barrow Wet (BW). For further details regarding LMM results, refer to Appendices S5 and S6.

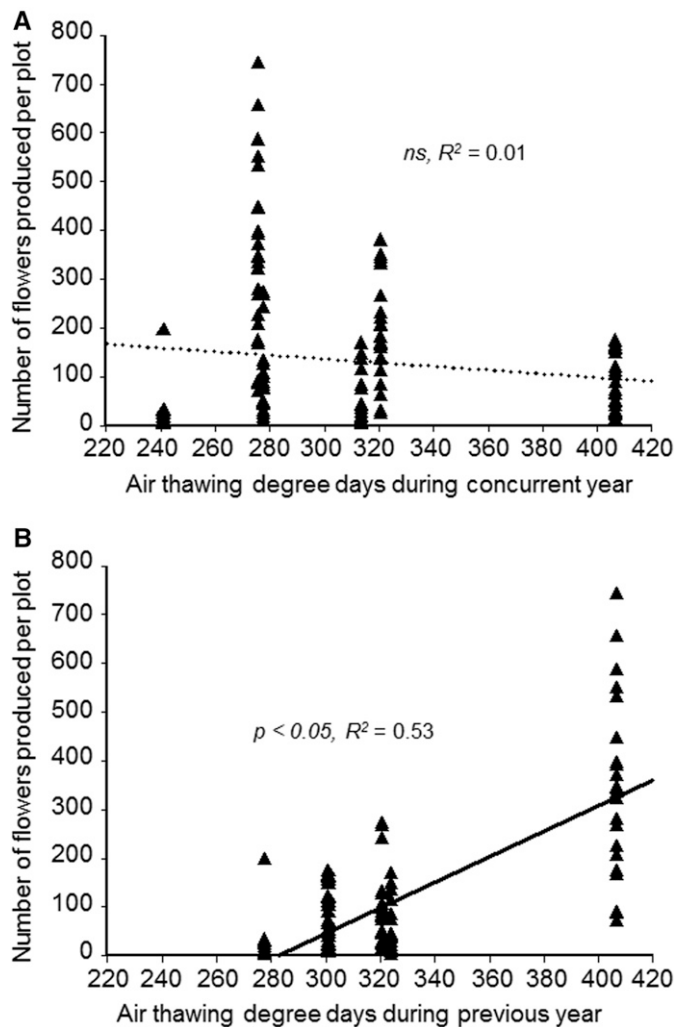


FIGURE 4 Comparative ability of thawing degree days to predict reproductive effort in *Cassiope tetragona* using temperature records from the (A) current and (B) previous year. Each point represents the total number of flowers in a plot at the BD site. The number of flowers produced and thawing degree days were significantly related when using temperature records from the previous field season (denoted with a solid line) but not when using temperature records of the current year (denoted with a dashed line). For further details regarding linear mixed model results, refer to Appendices S5 and S6.

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., 2010). 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 and 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 and 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 S1). We also observed tendencies toward warmer summer air and soil temperatures, warmer fall soil temperatures, and drier soils over time at all four 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 nonsignificant, tendencies parallel to those anticipated with climate change—The majority of our species showed nonsignificant tendencies toward increasing inflorescence heights and reproductive efforts over time (Fig. 2), which is consistent with general observations and predictions regarding arctic plant responses to climate change (Arft et al., 1999; Dormann and Woodin, 2002; ACIA, 2005; Hudson and 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 nonsignificant, tendencies toward increased reproductive efforts and larger inflorescences over time as species shift more resources into reproduction. For example, *Diapensia lapponica* at the Atkasuk 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 finding 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 and Woodin, 2002; Hollister et al., 2005a), other factors such as resource allocation strategies and responses to soil moisture need to be accounted for to develop accurate predictions for vegetation change.

Many plant traits are correlated with air and soil temperatures—In agreement with previous studies, our study 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., 2010). 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 during 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. 3). 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 and Jonasson, 1999).

Modifying degree day base temperatures improved our ability to predict plant responses to temperature—Arctic plants are well known for their phenotypic plasticity and sometimes demonstrate

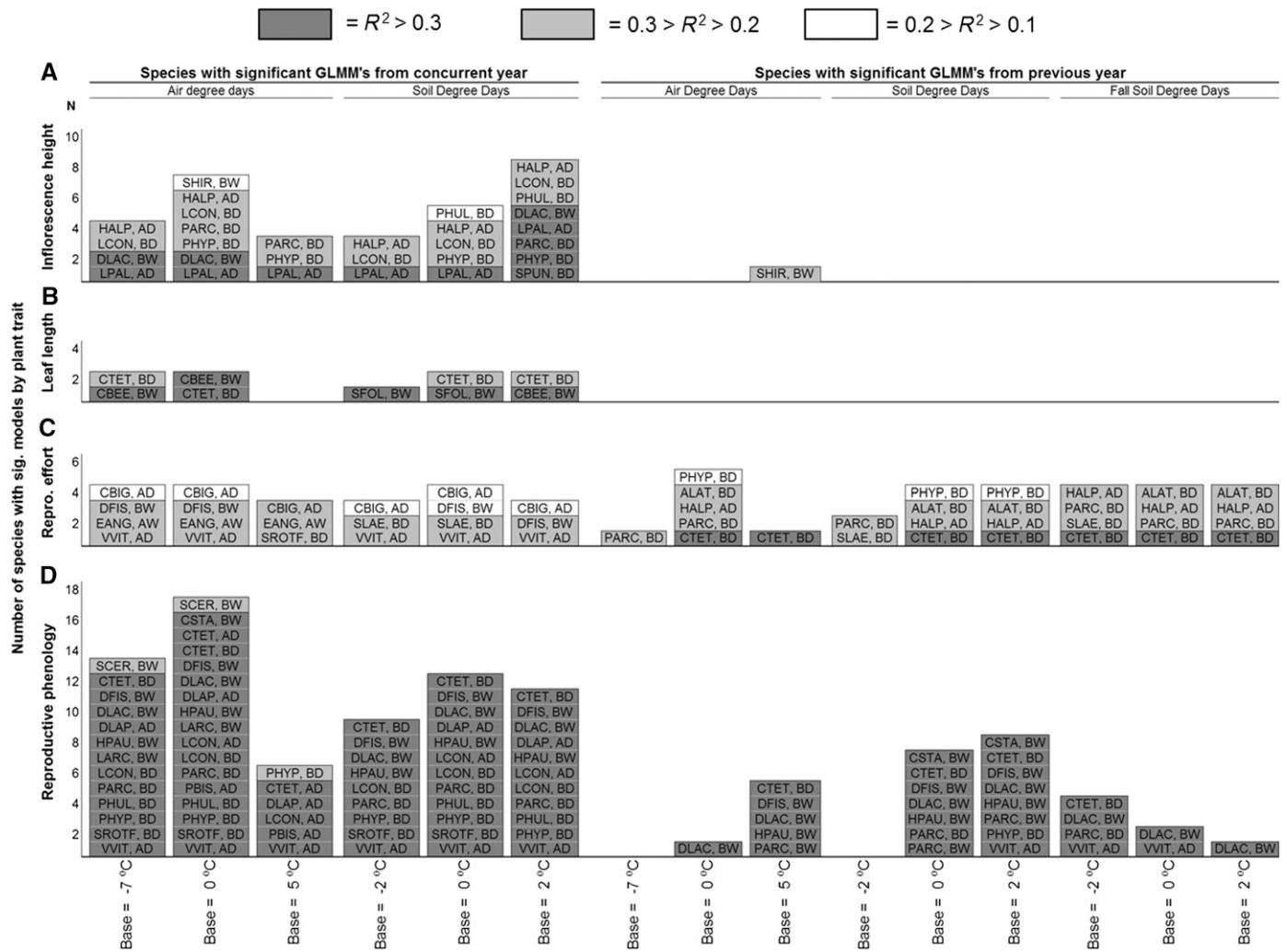


FIGURE 5 Comparative abilities of degree days calculated with different base temperatures to predict plant traits. Plant traits include (A) inflorescence length, (B) leaf length, (C) reproductive effort, and (D) reproductive phenology. Each bar represents one species showing a significant relationship with a given abiotic factor determined using linear mixed models (LMMs). Formatting follows Fig. 3, except slope sign is not indicated. Degree day base temperatures are indicated as “Base = $X^{\circ}\text{C}$,” with varying “ X ” values; for simplicity, we only present a subset of the base values; for the complete results, see Appendix S6. 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 S5 and S6.

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 Atkasuk 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 Atkasuk 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 approach 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 the approach described above due to the low number of species that occurred in multiple sites and showed 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 preadapted to grow at cold temperatures and that accounting for this ability 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

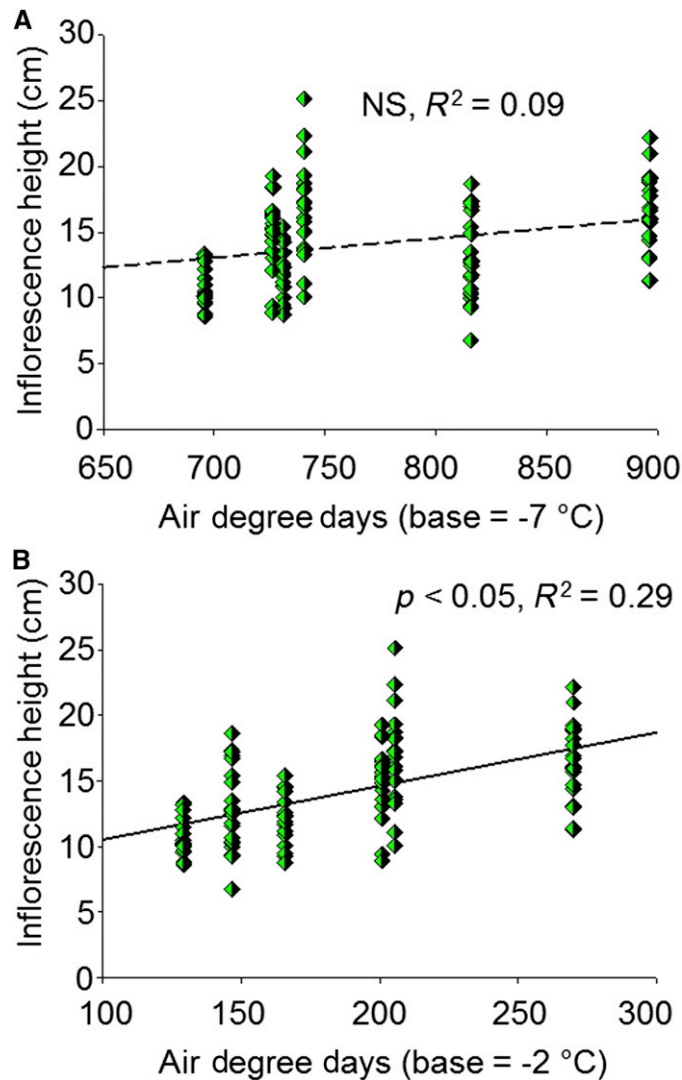


FIGURE 6 Predicting inflorescence heights for *Poa arctica* using different degree day base temperatures. Shown are the results of linear mixed models (LMMs) comparing inflorescence height to degree days of base temperatures of (A) -7°C and (B) 2°C . Each point represents average inflorescence height within a plot at the Barrow Dry site. Degree days and inflorescence height were significantly related when using a base temperature of 2°C (denoted with a solid line), but not when using a base temperature of -7°C (denoted with a dashed line). For further details regarding LMM results refer to Appendices S5 and S6.

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 adjustments to the degree day base temperature may reflect 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 effect into account because 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 three cases for which 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. 6). Future studies could compare actual tissue temperatures with 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 because some tundra plant species rely on cooling events to time flowering (Iler and 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. 3). 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 and Diggle, 2001). Sexual reproduction represents an enormous caloric investment compared with 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 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 use those resources during the consecutive year(s) for reproduction (Johnstone and 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 and 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 plant traits will respond to climate change 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 1). Interestingly, two of the

TABLE 1. 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 (LMMs) with air degree days as fixed effects and plot and year as random effects. Significant models were identified using a χ^2 likelihood ratio test with and without air degree days as an explanatory variable. These values were then subjected to a Benjamini–Hochberg procedure with a 5% false discovery rate (further detailed in the Materials and Methods). 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 and 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 LMMs presented in this study. Positive effect sizes signify increased inflorescence height, increased reproductive effort or delayed reproductive phenology.

Trait and site	Species	Effect size (Hedges' d)	LMM marginal R^2
Inflorescence height Barrow Dry	<i>Luzula confusa</i>	1.00	0.15
	<i>Poa arctica</i>	1.33	0.29
	<i>Potentilla hyparctica</i>	1.65	0.30
Reproductive effort Barrow Dry	<i>Cassiope tetragona</i>	0.84	0.53 ^a
	<i>Poa arctica</i>	0.37	0.25 ^a
Reproductive phenology Barrow Dry	<i>Cassiope tetragona</i>	−6.30	0.55
	<i>Luzula confusa</i>	−2.39	0.46
	<i>Papaver hultenii</i>	−5.62	0.58
	<i>Poa arctica</i>	−2.32	0.60
	<i>Potentilla hyparctica</i>	−7.55	0.44
Barrow Wet	<i>Luzula arctica</i>	−2.17	0.45

^a R^2 corresponds to the LMM using degree days during previous year.

species with traits that may be responding to climate change (*Cassiope tetragona* and *Poa arctica*) also showed an increase in percentage 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 and 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 variability 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; Pörnö 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 multilevel trophic interactions. Additionally, Lamb et al. (2011) showed that ecosystem interactions in the Arctic can be altered through poorly understood mechanisms because soil microbe communities respond to environmental shifts differently than plants. Furthermore, the addition of other abiotic factors (e.g., photosynthetically active radiation, nitrogen availability) may enable a better understanding of how arctic plants respond to climate change.

CONCLUSIONS

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 1980s (Hudson et al., 2011; Elmendorf et al., 2012a), and several studies show 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.

ACKNOWLEDGEMENTS

The authors thank Pat Webber and Christian Bay for beginning this project and the many field assistants who aided in collecting and analyzing these data, especially S. Elmendorf, J. May, J. Liebig, K. Kremers, and T. Botting. We also thank the National Science Foundation, Office of Polar Programs (OPP #9714103, #0632263, #0856516, #1432277), Barrow Arctic Science Consortium, and UMAIT for logistics, colleagues in the ITEX network for their supportive collaborations, and two thorough, anonymous reviewers for their comments. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

LITERATURE CITED

- ACIA. 2005. Impacts of a warming arctic: Arctic climate impact assessment. Cambridge University Press, Cambridge, UK.
- Aerts, R. 2006. The freezer defrosting: Global warming and litter decomposition rates in cold biomes. *Journal of Ecology* 94: 713–724.
- Åkerman, H. J., and M. Johansson. 2008. Thawing permafrost and thicker active layers in sub-arctic Sweden. *Permafrost and Periglacial Processes* 19: 279–292.
- Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. R. T. Dale, M. C. Diemer, et al. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs* 64: 491–511.
- Barrett, R. T., and R. D. Hollister. In press. Arctic plants are capable of sustained responses to long-term warming. *Polar Research*.

- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-8, available at <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: 401–578.
- Becklin, K. M., G. Gamez, B. Uelk, R. A. Raguso, and C. Galen. 2011. Soil fungal effects on floral signals, rewards, and aboveground interactions in an Alpine pollination web. *American Journal of Botany* 98: 1299–1308.
- Bliss, L. C. 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics* 2: 405–438.
- Brown, J., K. R. Everett, P. J. Webber, S. F. Maclean Jr., and D. F. Murray. 1980. The coastal tundra at Barrow. In J. Brown, P. C. Miller, L. L. Tieszen, and F. L. Bunnell [eds.], *An Arctic ecosystem: The coastal tundra at Barrow, Alaska*. 1–29. Dowden, Hutchinson, & Ross, Inc., Stroudsburg, Pennsylvania, USA.
- Callaghan, T. V., B. Å. Carlsson, and N. J. C. Tyler. 1989. Historical records of climate-related growth in *Cassiope tetragona* from the Arctic. *Journal of Ecology* 77: 823–837.
- Chapin, F. S., III, G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Response of arctic tundra to experimental and observed changes in climate. *Ecology* 76: 696–711.
- Chapin, F. S., III, M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire, et al. 2005. Role of land-surface changes in arctic summer warming. *Science* 310: 657–660.
- Chapin, F. S., III, and L. L. Tieszen, M. C. Lewis, P. C. Miller, and B. H. McCown. 1980. Control of tundra plant allocation patterns 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, Stroudsburg, Pennsylvania, USA.
- Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate change. *Ecology* 93: 1765–1771.
- Dormann, C. F., and S. J. Woodin. 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., J. Harte, and K. J. Taylor. 2003. Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. *Ecological Monographs* 73: 69–86.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, N. Boulanger-Lapointe, E. J. Cooper, et al. 2012a. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2: 453–457.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Björk, A. D. Björkman, T. V. Callaghan, L. S. Collier, et al. 2012b. Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecology Letters* 15: 164–175.
- Euskirchen, E. S., A. D. McGuire, and F. S. Chapin 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., H. Al Henry, C. N. Carlyle, S. R. White, C. Beierkuhnlein, J. F. Cahill, B. B. Casper, et al. 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.
- Hinkel, K. M., and 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: article 8168.
- Hinzman, L. D., N. Bettez, F. S. Chapin III, M. Dyurgerov, C. L. Fastie, B. Griffith, R. D. Hollister, et al. 2005. Evidence and implications of recent climate change in terrestrial regions of the Arctic. *Climatic Change* 72: 251–298.
- Hoffmann, A. A., J. S. Camac, R. J. Williams, W. Papst, F. C. Jarrad, and C. H. Wahren. 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., J. L. May, K. S. Kremers, C. E. Tweedie, S. F. Oberbauer, J. A. Liebig, T. F. Botting, et al. 2015. Warming experiments elucidate the drivers of observed directional changes in tundra vegetation. *Ecology and Evolution* 5: 1881–1895.
- Hollister, R. D., P. J. Webber, and C. Bay. 2005a. Plant response to temperature in northern Alaska: Implications for predicting vegetation change. *Ecology* 86: 1562–1570.
- Hollister, R. D., P. J. Webber, and C. E. Tweedie. 2005b. The response of Alaskan arctic tundra to experimental warming: Differences between short- and long-term responses. *Global Change Biology* 11: 525–536.
- Høye, T. T. 2014. Reducing uncertainty in species' responses to climate change. *Current Zoology* 60: 186–188.
- Høye, T. T., E. Post, H. Meltofte, N. M. Schmidt, and M. C. Forchhammer. 2007. Rapid advancement of spring in the High Arctic. *Current Biology* 17: R449–R451.
- Hudson, J. M. G., and G. H. R. Henry. 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. *Ecology* 90: 2657–2663.
- Hudson, J. M. G., G. H. R. Henry, and W. K. Cornwell. 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., and D. W. Inouye. 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, UK.
- Johnstone, J., and G. H. R. Henry. 1997. Retrospective analysis of growth and reproduction in *Cassiope tetragona* and relations to climate in the Canadian High Arctic. *Arctic and Alpine Research* 29: 459–469.
- Jorgenson, M. T., Y. L. Shur, and E. R. Pullman. 2006. Abrupt increase in permafrost degradation in Arctic Alaska. *Geophysical Research Letters* 33: L02503.
- Kattge, J., S. Díaz, S. Lavorel, C. Prentice, P. Leadley, G. Bönisch, E. Garnier, et al. 2011. TRY—A global database of plant traits. *Global Change Biology* 17: 2905–2935.
- Kittel, T. G. F., B. B. Baker, J. V. Higgins, and J. C. Haney. 2010. Climate vulnerability of ecosystems and landscapes on Alaska's North Slope. *Regional Environmental Change* 11: 249–264.
- Klady, R. A., G. H. R. Henry, and V. Lemay. 2010. Changes in high arctic tundra plant reproduction in response to long-term experimental warming. *Global Change Biology* 17: 1611–1624.
- Lamb, E. G., S. Han, B. D. Lanoil, G. H. R. Henry, M. E. Brummell, S. Banerjee, and S. D. Siciliano. 2011. A High Arctic soil ecosystem resists long-term environmental manipulations. *Global Change Biology* 17: 3187–3194.
- Marchand, F. L., I. Nijs, M. Heuer, S. Mertens, F. Kockelbergh, J. Y. Pontailier, I. Impens, and L. Beyens. 2004. Climate warming postpones senescence in High Arctic tundra. *Arctic, Antarctic, and Alpine Research* 36: 390–394.
- Marion, G. M., G. H. R. Henry, D. W. Freckman, J. Johnstone, G. Jones, M. H. Jones, E. Lévesque, U. Molau, P. Mølgaard, A. N. Parsons, J. Svoboda, and R. A. Virginia. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology* 3: 20–32.
- McKane, R. B., L. C. Johnson, G. R. Shaver, K. J. Nadelhoffer, E. B. Rastetter, B. Fry, A. E. Giblin, et al. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415: 68–71.
- Meloche, C. G., and P. K. Diggle. 2001. Preformation, architectural complexity, and developmental flexibility in *Acomastylis rossii* (Rosaceae). *American Journal of Botany* 88: 980–991.
- Molau, U., U. Nordenhall, and B. Eriksen. 2005. Onset of flowering and climate variability in an alpine landscape: A 10-year study from Swedish Lapland. *American Journal of Botany* 92: 422–431.
- Oberbauer, S. F., S. C. Elmendorf, T. G. Troxler, R. D. Hollister, A. V. Rocha, M. S. Bret-Harte, M. A. Dawes, et al. 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 368: 20120481.

- Park, H., H. Yabuki, and T. Ohata. 2012. Analysis of satellite and model datasets for variability and trends in Arctic snow extent and depth, 1948–2006. *Polar Science* 6: 23–37.
- Pornon, A., N. Escaravage, and T. Lamaze. 2007. Complementarity in mineral nitrogen use among dominant plant species in a subalpine community. *American Journal of Botany* 94: 1778–1785.
- Post, E., and M. C. Forchhammer. 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., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, et al. 2009. Ecological dynamics across the Arctic associated with recent Climate Change. *Science* 325: 1355–1358.
- R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Savile, D. B. O. 1972. Arctic adaptations in plants. *Canadian Department of Agriculture Monograph* 6: 1–81.
- Serreze, M. C., J. E. Walsh, F. S. Chapin III, T. Osterkamp, M. Dyurgerov, V. Romanovsky, W. C. Oechel, J. Morison, T. Zhang, and R. G. Barry. 2000. Observational evidence of recent change in the northern high-latitude environment. *Climatic Change* 46: 159–207.
- Shaver, G. R., and S. Jonasson. 1999. Response of arctic ecosystems to climate change: Results of long-term field experiments in Sweden and Alaska. *Polar Research* 18: 245–252.
- Shiklomanov, N. I., D. A. Streletskiy, F. E. Nelson, R. D. Hollister, V. E. Romanovsky, C. E. Tweedie, J. G. Bockheim, and J. Brown. 2010. Decadal variations of active-layer thickness in moisture-controlled landscapes, Barrow, Alaska. *Journal of Geophysical Research—Biogeosciences* 115: G00104.
- Sørensen, T. 1941. Temperature relations and phenology of northeast Greenland flowering plants. *Meddelelser om Grønland* 125: 1–305.
- Soudzilovskaia, N. A., T. G. Elumeeva, V. G. Onipchenko, I. I. Shidakov, F. S. Salpagarova, A. B. Khubiev, D. K. Tekeev, and J. H. C. Cornelissen. 2013. Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proceedings of the National Academy of Sciences, USA* 110: 18180–18184.
- Stenström, A., I. S. Jónsdóttir, and M. Augner. 2002. Genetic and environmental effects on morphology in clonal sedges in the Eurasian Arctic. *American Journal of Botany* 89: 1410–1421.
- Stone, R. S., E. G. Dutton, J. M. Harris, and D. Longenecker. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change. *Journal of Geophysical Research—Atmospheres* 107: D10.
- Stow, D. A., A. Hope, D. McGuire, D. Verbyla, J. Gamon, F. Huemmrich, S. Houston, et al. 2004. Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing of Environment* 89: 281–308.
- Tape, K., M. Sturm, and C. Racine. 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., P. J. Webber, E. H. Arnold, and D. Ebert-May. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology* 75: 393–408.
- Wendler, G., B. Moore, and K. Galloway. 2014. Strong temperature increase and shrinking sea ice in Arctic Alaska. *Open Atmospheric Science Journal* 8: 7–15.
- Wheeler, H. C., T. T. Høye, N. M. Schmidt, J.-C. Svenning, and M. C. Forchhammer. 2015. Phenological mismatch with abiotic conditions—Implications for flowering in Arctic plants. *Ecology* 96: 775–787.
- Zeng, H. Q., G. S. Jia, and H. Epstein. 2011. Recent changes in phenology over the northern high latitudes detected from multi-satellite data. *Environmental Research Letters* 6: 045508.