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ARTICLE

Long-term effects of snowmelt timing and climate warming on phenology, growth, and reproductive effort of Arctic tundra plant species[1]

Esther R. Frei and Gregory H.R. Henry

Abstract: Arctic regions are particularly affected by rapidly rising temperatures and altered snow regimes. Snowmelt timing depends on spring temperatures and winter snow accumulation. Scenarios for the Arctic include both decreases and increases in snow accumulation. Predictions of future snowmelt timing are, thus, difficult and experimental evidence for ecological consequences is scarce. In 1995, a long-term factorial experiment was set up in a High Arctic evergreen shrub heath community on Ellesmere Island, Canada. We investigated how snow removal, snow addition, and passive warming affected phenology, growth and reproductive effort of the four common tundra plant species *Cassiope tetragona* (L.) D. Don, *Dryas integrifolia* Vahl, *Luzula arctica* Blytt, and *Papaver radicatum* Rottb. Timing of flowering and seed maturation as well as flower production were more strongly influenced by the combined effects of snowmelt timing and warming in the two shrub species than in the two herbaceous species. Warming effects persisted over the course of the growing season and resulted in increased shrub growth. Moreover, the long-term trend of increasing growth in two species suggests that ambient warming promotes tundra plant growth. Our results confirm the importance of complex interactions between temperature and snowmelt timing in driving species-specific plant responses to climate change in the Arctic.

Key words: Alexandra Fiord, experimental warming, experimental snow manipulation, phenology, growth and reproductive traits, International Tundra Experiment (ITEX).

Résumé : Les régions arctiques sont particulièrement touchées par la hausse rapide des températures et la modification des régimes de neige. Le moment de la fonte des neiges dépend des températures printanières et de l'accumulation de neige en hiver. Les scénarios pour l'Arctique comprennent à la fois des diminutions et des augmentations de l'accumulation de neige. Il est ainsi difficile de prédire le moment de la fonte des neiges et les preuves expérimentales de conséquences écologiques sont rares. En 1995, une expérience factorielle à long terme a été mise en place dans une communauté d'arbustes éricacées sempervirents du Haut-Arctique sur l'île d'Ellesmere, au Canada. Les auteurs ont étudié comment l'enlèvement de la neige, l'ajout de neige et le réchauffement passif affectaient la phénologie, la croissance et l'effort de reproduction des quatre espèces végétales communes de la toundra : *Cassiope tetragona* (L.) D. Don, *Dryas integrifolia* Vahl, *Luzula arctica*

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Blytt, et *Papaver radicatum* Rottb. Le moment de la floraison et de la maturation des graines ainsi que la production de fleurs étaient plus fortement influencés par les effets combinés du moment de la fonte des neiges et du réchauffement chez les deux espèces d'arbustes que chez les deux espèces herbacées. Les effets du réchauffement persistaient au cours de la saison de croissance et entrainaient une augmentation de la croissance des arbustes. De plus, la tendance à long terme de l'augmentation de la croissance chez deux espèces suggère que le réchauffement ambiant favorise la croissance des plantes de la toundra. Ces résultats confirment l'importance des interactions complexes entre la température et le moment de la fonte des neiges dans les réponses spécifiques à l'espèce des végétaux de l'Arctique face aux changements climatiques. [Traduit par la Rédaction]

Mots-clés : Alexandra Fiord, réchauffement expérimental, manipulation expérimentale de la neige, phénologie, traits de croissance et de reproduction, expérience internationale sur la toundra (ITEX).

Introduction

Snow is a characteristic seasonal feature of the Arctic land surface that influences the energy balance and the availability of resources such as water, light, and nutrients essential for plant life, soil communities, and terrestrial animals (Callaghan et al. 2011). Snowmelt is considered to be the start of the growing season in tundra ecosystems, and the timing depends on both spring temperatures and the accumulation of snow during winter and its distribution, which is affected by factors such as wind and topography (Bjorkman et al. 2015; Bokhorst et al. 2016). Predicted changes in Arctic snow cover with climate change vary by season and region (Dauginis and Brown 2021). There is evidence that warming leads to a trend towards a later start of the snow season in many regions of the Arctic (Brown et al. 2017), and in some regions, also to earlier snowmelt in spring (Derksen and Brown 2012; Hernández-Henríquez et al. 2015). Temperature signals are much clearer: global average temperature increased by 0.9 °C over the last century (1901–2012) with the past three decades being successively warmer than any of the previous decades in the instrumental record (Stocker et al. 2013). Arctic regions experienced up to three times greater warming and climate projections predict further substantial annual and winter warming for the region (IPCC 2018; Meredith et al. 2019; AMAP 2021).

Although these predictions for pronounced future warming are consistent throughout Arctic latitudes, estimates of temporal and spatial changes in precipitation patterns are much less certain (ACIA 2004; Meredith et al. 2019). Increasing winter temperature and winter precipitation have resulted in increased snow depths over the Scandinavian and Eurasian Arctic (Callaghan et al. 2011), but by contrast, weather station records so far reveal no significant snowfall trends for the North American High Arctic (Bokhorst et al. 2016; AMAP 2017). In addition, remote sensing and land surface models identify mostly negative trends in snow water equivalent for the whole Arctic (Vincent et al. 2015; Brown et al. 2017). Increased winter snowfall in many Arctic regions (Callaghan et al. 2011) may lead to delayed snowmelt and shorter or unchanged growing season lengths (Cooper et al. 2011; Meredith et al. 2019), unless there are substantially warmer spring temperatures. Thus, it remains open whether snowmelt dates will advance, remain relatively unchanged, or be delayed in the future, and this will likely vary across the Arctic.

Arctic ecosystems are particularly vulnerable to rapid and major changes, which drastically alter the environmental conditions of Arctic species (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Post et al. 2009; Bjorkman et al. 2018; Panchen et al. 2021). Warming responses of tundra plant species and communities have been widely studied and patterns described in syntheses include changes in community composition (Walker et al. 2006; Elmendorf et al. 2012*a*; Elmendorf et al. 2012*b*), increased growth and

reproduction (Arft et al. 1999; Hudson et al. 2011; Klady et al. 2011; Panchen et al. 2021), as well as altered phenology (Bjorkman et al. 2015; Prevey et al. 2017; Post et al. 2018). Plant responses to warming also differ among functional groups and species (Elmendorf et al. 2012*a*; Assmann et al. 2019; Prevey et al. 2019), which may be partly due to the influence of additional drivers. In addition to warming, snowmelt timing has been identified as another key driver of Arctic plant life (Assmann et al. 2019; Bjorkman et al. 2020) that may interact with the effects of warming (Bjorkman et al. 2015). It determines the start of the growing season and ultimately the character of tundra plant communities (Billings and Mooney 1968; Wipf and Rixen 2010; Cooper et al. 2011; Bjorkman et al. 2015; Rixen et al. 2021). Earlier snowmelt advances spring phenology in Arctic ecosystems (Høye et al. 2007; Wipf et al. 2009; Assmann et al. 2019), which may also result in mismatches with pollinators (Høye et al. 2013; Cooper 2014) and increased susceptibility to freezing events when the protective snow cover disappears earlier in the year (Jonas et al. 2008; Wipf et al. 2009; Slatyer et al. 2021). Earlier snowmelt has also been shown to increase growth, productivity, and reproduction of tundra species by the extension of the growing season (Høye et al. 2007; Wipf et al. 2009; Cooper et al. 2011; Mallik et al. 2011; Semenchuk et al. 2013). In combination with warmer temperatures, decreasing snow cover may alter the functional composition and diversity of Arctic tundra communities (Niittynen et al. 2018, 2020). Delayed snowmelt, by contrast, is likely to delay phenology (Bjorkman et al. 2015; Assmann et al. 2019) and, because of a shortened or shifted growing season, can result in reduced reproductive effort and success, abundance, and aboveground biomass in Arctic ecosystems (Cooper et al. 2011; Semenchuk et al. 2013). Responses of High Arctic plants to changed snow conditions can be highly species specific (Rumpf et al. 2014; Assmann et al. 2019).

In addition to such direct effects, snow cover affects ecological interactions indirectly as postulated by the snow–shrub hypothesis stating that shrub abundance is greater in areas with more snow accumulation (Sturm et al. 2001), as was observed in a snow fence experiment at Toolik Lake after 20 years of treatment (Leffler et al. 2016). Snow trapping by shrubs leads to higher soil temperatures in winter and subsequently enhanced soil microbial activity that may be responsible for increasing soil nitrogen availability and, in turn, greater shrub growth (Sturm et al. 2005; Vankoughnett and Grogan 2014). This can produce a positive feedback loop in which increased snow trapping in shrubby plant communities leads to improved growing conditions for shrubs (Sturm et al. 2001; Morgner et al. 2010; Leffler and Welker 2013). Observations of increasing shrub abundance over time throughout the Arctic support this hypothesis (Tape et al. 2006; Jia et al. 2009; Forbes et al. 2010; Myers-Smith et al. 2011; Berner et al. 2020; Myers-Smith et al. 2020). These changes in vegetation structure also affect interactions with other trophic levels in tundra systems (Ims and Fuglei 2005; Kytoviita and Ruotsalainen 2007; Post and Forchhammer 2008; Van der Putten et al. 2010).

Although the individual effects of warming and snowmelt timing have been repeatedly tested in manipulative experiments as well as in observational studies along natural gradients (synthesized in Wipf and Rixen 2010; Elmendorf et al. 2012*a*; Bjorkman et al. 2020; Rixen et al. 2021), studies combining manipulations of both drivers are scarce (but see Keuper et al. 2011; Gillespie et al. 2016; Leffler et al. 2016; Livensperger et al. 2016). We investigated phenology, growth, and reproductive effort of two shrub and two herbaceous plant species in response to 21 years of experimental warming, snow removal (advanced snowmelt), and snow addition (delayed snowmelt). To the best of our knowledge, this is the longest-running factorial experiment in a High Arctic tundra ecosystem testing the individual and combined effects of snowmelt timing and warming. Specifically, we ask (*i*) how have changes in snowmelt timing and elevated temperatures affected

phenology, growth and reproductive effort of Arctic plant species over the past 21 years?; (*ii*) are the effects of earlier snowmelt on plant traits more pronounced under elevated temperatures?; (*iii*) does delayed snowmelt reduce effects of experimental warming?; and (*iv*) do these responses differ among species?

We predict that both earlier snowmelt and experimental warming lead to advances in phenology, increased growth, and enhanced flower production across species. Furthermore, we expect enhanced plant responses when earlier snowmelt and warming are combined. However, if snowmelt is delayed due to increased winter snow depths, we expect that the warming effects are dampened resulting in unchanged or even delayed spring phenology, and unchanged or reduced growth and flower production across species.

Materials and methods

Study site and species

The Alexandra Fiord coastal valley (78°53′N, 75°55′W) is a ~8 km^2 glacial sandur with heterogeneous tundra habitats on the east-central coast of Ellesmere Island, Nunavut in the Canadian High Arctic. It is bounded on two sides by low mountains (500–700 m above sea level), to the south by mountains and the Twin Glacier, and to the north by Alexandra Fiord. Although the surrounding area is dominated by polar desert landscapes due to low precipitation levels, cooler temperatures, and poor soil development (Freedman et al. 1994), the Alexandra Fiord valley supports a relatively diverse assemblage of species and habitats in part due to greater soil moisture availability as a result of greater snow cover and microtopographic controls on snow distribution and glacial runoff (Muc et al. 1989; Freedman et al. 1994). Our study was conducted on a homogeneous site with a relatively long-lasting seasonal snow cover. Vascular plants covered up to 75% of the ground surface, whereas the remaining 25% consisted of bryophytes, bare ground, and rocks (Hudson and Henry 2009, 2010). The mesic shrub–heath community at the site is dominated by the evergreen dwarf-shrubs *Cassiope tetragona* (L.) D. Don (Arctic white heather) and *Dryas integrifolia* Vahl (mountain avens, Muc et al. 1989), and these species were also two of the study species. In addition, we chose the common forb *Papaver radicatum* Rottb. (rooted poppy) and the graminoid *Luzula arctica* Blytt (Arctic wood rush) as study species. The four species represent three different functional types, are abundant at the study site, and are widespread throughout the Arctic and subarctic (Porsild and Cody 1980).

Experimental design

In 1992, a passive warming experiment was established consisting of 24 1 m^2 plots with hexagonal open-top chambers (OTCs) randomly assigned to half of them. OTCs were constructed of clear fiberglass (1992–2009) and plexiglass (2009–present) sheets 0.5 m high and inclined to 60°, enclosing 1.8 m^2. The experimental studies at Alexandra Fiord were the first to be established as part of the International Tundra Experiment (ITEX) (Henry and Molau 1997). In 1995, 12 more plots were established for a full factorial experiment combining passive warming with snow removal and snow addition treatments on 36 plots. Treatments (warming by OTC × snow manipulation) were randomly assigned to experimental plots resulting in six replications for each of the six treatment combinations (Supplementary Table S1[1]). The OTCs have remained on the plots throughout the years and snow depth was modified before the beginning of the growing season by carefully removing snow from designated plots (snow removal plots) and adding it to other plots (snow addition plots). The experiment was run from 1995 through 2015. Natural snow depth

[1]Supplementary data are available with the article at https://doi.org/10.1139/as-2021-0028.

at the time when the snow manipulations were applied was usually 20–30 cm. Due to delays in arrival and other research priorities at the site, snow treatments could not be applied in the years 2006 and 2009–2013. In removal plots snow was carefully removed and a thin snow layer was left to not damage plants. The snow in these plots usually melted within 1 day after snow removal. In snow addition plots, approximately 20 cm of snow was added on top of the natural snow cover, thereby roughly doubling the snow depth at time of treatment.

Climate data and snowmelt observations

Ambient air temperature at 1.5 m height was measured at a climate station approximately 250 m from the experimental site. Temperature readings were taken every 5 min and data recorded on a data logger (CR10; Campbell Scientific Canada Corp., Edmonton, AB, Canada). Raw data were first aggregated to daily means and based on these daily values, seasonal averages were calculated for the growing season (Day of Year (DOY) 150–224) and the non-growing season (DOY 225–149) as the arithmetic mean of the daily values. Ultrasonic snow-depth sensors (UDG01; Campbell Scientific Canada Corp., Edmonton, Canada) were installed over four experimental plots that did not receive snow treatments (2 OTCs and 2 control plots), connected to a datalogger (CR10; Campbell Scientific Canada Corp.) and measurements were recorded twice a day. We report annual maximum snow depths for OTCs and for control plots (all plots without snow treatments). An earlier analysis of these measurements found no changes in snow depth for the first ten years (1993–2002) of the experiment (Hudson and Henry 2009). We report total winter snow accumulation and snow depth at the end of April and the end of May at the Environment Canada weather station Eureka, approximately 240 km northwest of Alexandra Fiord, because both temperature records and snow observations at the two sites are well correlated (Labine 1994; Bjorkman et al. 2015). Snowmelt dates were determined by daily visual observations of the experimental plots from arrival at the site until complete snowmelt. Snowmelt date was defined as the date when the visually estimated proportion of plot area covered by snow fell below 10%. Snowmelt could not be recorded in 2006 and 2009 due to late arrival at the site.

Trait measurements

In each plot, several individuals of each study species were chosen randomly. A single branch in separate plants for *C. tetragona* and single plants for the three other species were well marked to ensure that the same individuals were monitored each time. The number of individuals per plot varied between two and five depending on the species. These individuals were tagged permanently with aluminum labels for comprehensive long-term monitoring (for details see Supplementary Table S2[1]). The monitoring was continued on a nearby replacement individual when a tagged individual died or a tag became detached from the originally selected individual. We determined the dates of first mature flower and first mature seed by assessing the phenological stage of marked individuals every 3–4 days, but in some years the time between sampling was 6 days or more towards the end of the growing season. Mature flower was defined as fully open corolla (*C. tetragona*, *P. radicatum* and *D. integrifolia*) and as flower with visible pistils and stamens (*L. arctica*). We also recorded the date on which mature seeds were first observed, i.e., when the seed capsules of *L. arctica* became dark brown and began to split, when styles of *D. integrifolia* seed capsules elongated and twisted, and when the first capsule of *P. radicatum* opened. For *C. tetragona,* we recorded the date when bent down seed capsules formed. The height of the tallest flowering shoots of each tagged individual of *P. radicatum*, *D. integrifolia* and *L. arctica* was measured at the peak of the flowering period from the base of the plant

to the base of the flower. In *C. tetragona*, the tip of the tagged main shoot was marked with water-based, non-toxic correction fluid before leaf bud break and then, the length of the annual growth increment was measured with calipers (to an accuracy of about 0.1–0.2 mm) in the first half of August, after which temperature at the site rapidly falls and the growing season ends (Rayback and Henry 2005). Flower densities were recorded by counting the total number of flowers per species within a 1 m^2 square positioned over permanent corner markers in the centre of each plot in the second half of July when the majority of flowers had reached maturity.

Statistical analyses

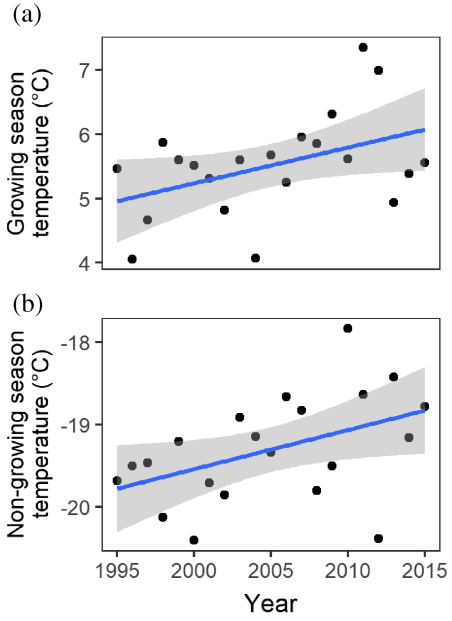
To assess trends in seasonal temperature averages, total winter snow accumulation and snow depths over the 21 years of the study (1995–2015), we calculated simple linear regressions of these weather variables against the year of observation. The change in snowmelt date was determined using a linear mixed model, where year (a continuous variable), was included as fixed effect. Random effects of plot and year were included to account for the nonindependence of measurements from the same plot over time and of all plots measured in the same year. Linear and generalized linear mixed-effects models (Pinheiro and Bates 2000; Faraway 2006) were used to analyse the responses of phenological, growth, and reproductive traits. Gaussian models were used to fit the data of the phenological and growth traits, whereas negative binomial models were used for the flower density data because of strong overdispersion in these count data (overdispersion parameters between 2.75 and 3.77). Snow treatment, warming treatment, and their interaction were included in the models as fixed effects. Year and plot were included as random effects to account for temporal correlation within year and for spatial correlation among individuals in the same plot. Models were fitted using the package glmmTMB (Brooks et al. 2017) and model diagnostics to check for outliers, uniformity of residuals, and overdispersion was performed with the package DHARMa (Hartig 2020) in R 3.6.3 (R Development Core Team 2020). Significances of model factors were determined by Wald z-Tests. We calculated simple regressions of plant traits against year for the full control plots only to investigate long-term trends in phenology, growth and reproductive effort due to environmental changes over the 21 years of the study. We also calculated simple regressions of plant traits against individual plot snowmelt date and average growing season temperature.

Results

Air temperature, snow depth, and timing of snowmelt

Measurements at Alexandra Fiord show a significant increase in growing season air temperatures over the past two decades from 1995 to 2015 despite substantial year-to-year variation (+0.51 °C/decade, $R^2 = 0.17$, $p = 0.03$; Fig. 1*a*). Non-growing season air temperatures (DOY 225–149) increased at nearly the same rate of +0.49 °C/decade ($R^2 = 0.22$, $p = 0.01$) between 1995 and 2015 (Fig. 1*b*). Annual maximum snow depths at the experimental site revealed a slight, but non-significant, decreasing trend between 1995 and 2015 (–4.6 cm/decade, $R^2 = 0.06$, $p = 0.18$; Fig. 2*b*), whereas total winter snowfall at the nearby weather station Eureka has slightly, but non-significantly, increased (+3.7 cm/decade, $R^2 = –0.02$, $p = 0.48$; Fig. 2*a*). Considering all available data (1950–2015), there was a similar and highly significant increase in winter snow depths measured at Eureka (+4.0 cm/decade, $R^2 = 0.24$, $p < 0.001$; Supplementary Fig. S1[1]). Snow depths at Eureka at the end of May showed a slight but non-significant increasing trend between 1995 and 2015 (+1.2 cm/decade, $R^2 = –0.03$, $p = 0.51$; Fig. 2*a*). Average annual maximum snow depth in the OTCs (43.9 ± 8.6 cm) was 9.5 ± 4.4 cm (28%) greater than in control plots (43.9 ± 8.6 cm vs. 34.3 ± 8.9 cm; Supplementary Fig. S2[1]).

Fig. 1. Annual average growing season air temperature (*a*) and non-growing season air temperature (*b*) at Alexandra Fiord (1995–2015). Average growing season temperature (June to August; Day of Year 150–224) increased by 0.51 °C/decade ($R^2 = 0.17$, $p = 0.03$) and average non-growing season temperature (September to May; Day of Year 225–149) increased by 0.49 °C/decade ($R^2 = 0.22$, $p = 0.01$). Solid lines show significant linear fits of the data and 95% confidence intervals are shaded.

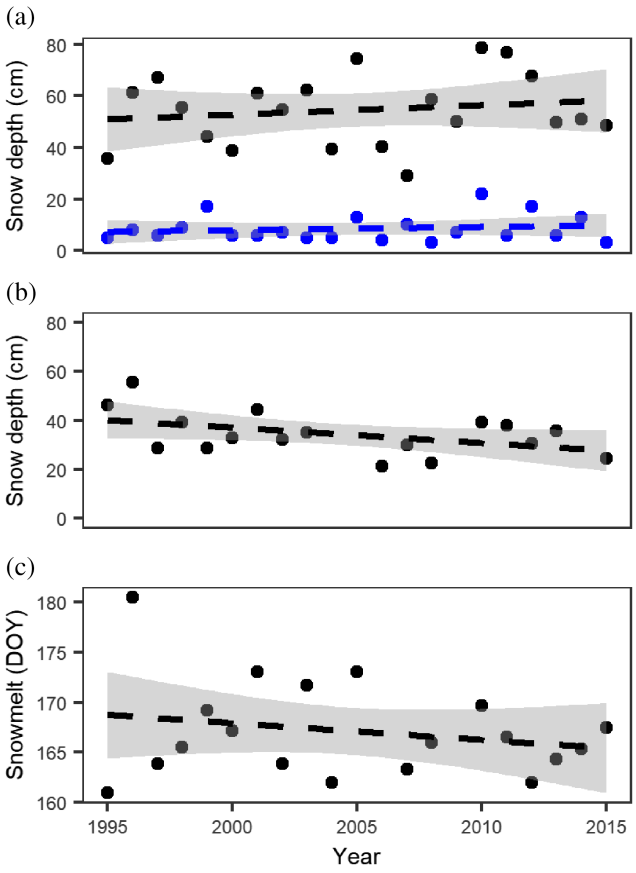


Over the whole observation period from 1995 to 2015 snowmelt in the full control plots occurred on average on day 167, with no clear trend over the 21-year observation period (–1.7 days/decade, $R^2 = –0.01$, $p = 0.36$; Fig. 2*b*). The earliest average snowmelt in these plots occurred on day 161 in 1995 and the latest average snowmelt on day 181 in 1996. The warming treatment did not affect snowmelt timing ($p > 0.1$; Figs. 3*a*, 4*a*). In the years when the snow manipulations were applied (1995–2005, 2007–2008, and 2014–2015), there was a significant effect of the snow treatment on snowmelt dates ($p < 0.001$; Figs. 3*b*, 4*a*) with snowmelt occurring 2.0 days earlier in snow removal plots than in the control plots, but 2.5 days later in snow addition plots than in the control plots. There was no difference in snowmelt timing between snow addition, control, and snow removal plots in years without snow manipulation treatment (i.e., 2010–2013; Fig. 4*b*), confirming that the assignment of snow treatments to plots was unbiased.

Phenology

Experimental warming advanced flowering of *C. tetragona* by 2.4 days ($p = 0.003$; Fig. 5*a* and Table 1) and of *D. integrifolia* by 1.8 days ($p = 0.006$; Fig. 5*b*). There was also a slight trend of advanced flowering of *L. arctica* in warmed plots ($p = 0.09$; Fig. 5*c*). Snow treatment had a clear effect on *C. tetragona* with 1.8 days advanced flowering in removal plots ($p = 0.03$) and 1.6 days delayed flowering in addition plots ($p = 0.04$; Fig. 5*a*). There was also a tendency towards earlier flowering of *L. arctica* in snow removal plots ($p = 0.06$; Fig. 5*c*). In *D. integrifolia* and *P. radicatum*, marginally significant interactions between warming and snow removal were observed with advanced flowering in warmed but not in control plots ($p = 0.07$ and $p = 0.08$; Fig. 5*b*, and 5*d*). Under ambient climate conditions, flowering start of all study species remained unchanged over the past 21 years ($p > 0.49$; Supplementary Fig. S3[1]).

Fig. 2. Snow depth at Eureka (*a*), maximum snow depth at Alexandra Fiord (*b*), and snowmelt dates (*c*) for the time period of the experiment 1994/1995–2014/2015. Panel (*a*): Total winter snow accumulation in black (+3.7 cm/decade, $R^2 = -0.02$, $p = 0.48$) and snow depth at the end of May of each year in blue (+1.2 cm/decade, $R^2 = -0.03$, $p = 0.51$) at Eureka, an Environment Canada weather station on western Ellesmere Island. Panel (*b*): Annual maximum snow depth in the full control plots at Alexandra Fiord (−6.2 cm/decade, $R^2 = 0.15$, $p = 0.07$). Black dots show the average of two snow depth sensors. Panel (*c*): Average yearly snowmelt dates in the full control plots of the study site from visual observations (−1.7 days/decade, $R^2 = -0.01$, $p = 0.36$). Dashed lines show non-significant linear fits of the data and 95% confidence intervals are shaded. Snowmelt observations from 2006 and 2009 are missing. DOY, Day of Year.



However, higher average growing season temperatures were correlated with earlier flowering start in *C. tetragona*, *D. integrifolia* and *P. radicatum* ($p \leq 0.003$). Earlier snowmelt dates were correlated to earlier flowering in *D. integrifolia* and *L. arctica* ($p \leq 0.007$).

Fruits or seeds in all species appeared approximately 4 days earlier in warming-only treatments ($p \leq 0.02$), except *L. arctica* ($p = 0.43$; Fig. 5 and Table 1). In snow addition plots, the formation of seeds was delayed, on average, by 3.5 days in *D. integrifolia* ($p = 0.02$; Fig. 5*f*) and 2.2 days in *L. arctica* ($p = 0.02$; Fig. 5*g*). In snow removal plots, fruit formation was advanced by 4.0 days in *C. tetragona* ($p < 0.001$; Fig. 5*e*). There was also a tendency towards advanced formation of seed capsules by 3.1 days in *P. radicatum* ($p = 0.06$; Fig. 5*g*), but not in the other two species. Over the study period of 21 years, the timing of seed maturation did not shift under ambient climate conditions ($p > 0.35$; Supplementary Fig. S3[1]). Higher average growing season temperatures correlated with advanced seed formation in

Fig. 3. Yearly average snowmelt dates in response to warming (*a*) and snow treatments (*b*) over the period of the experiment (1995–2015). Treatment years are indicated with red and blue bars. Snowmelt observations from 2006 and 2009 are missing. Error bars indicate standard errors among plots. DOY, Day of Year; OTC, Open Top Chamber.

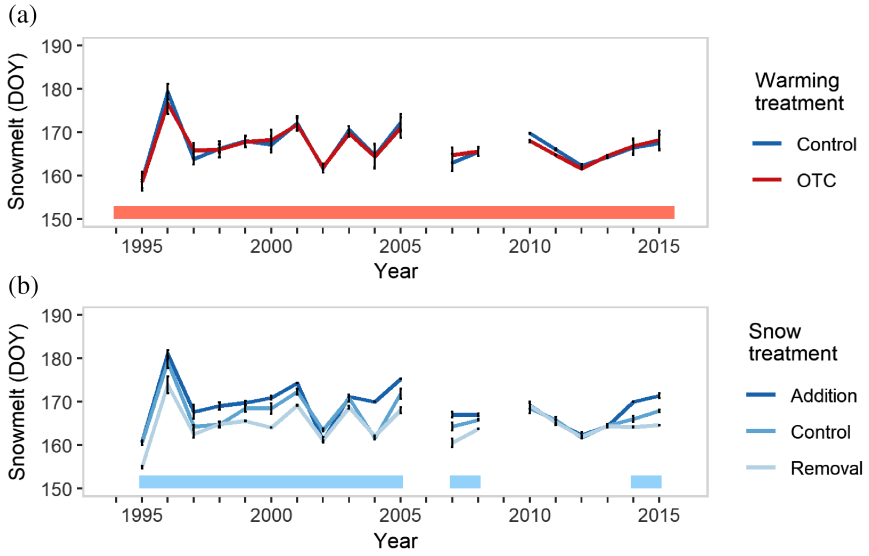
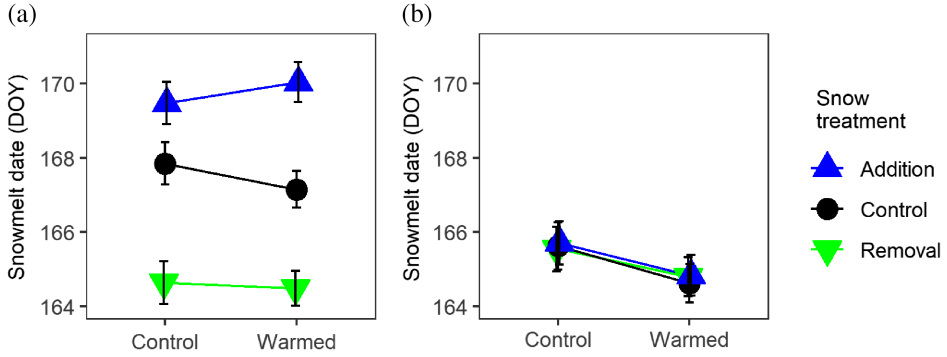


Fig. 4. Effects of snow and warming treatments on average snowmelt dates in years when snow treatments were applied (*a*) and in years 2006, 2009–2013 when snow treatments were not applied (*b*). Data are means with standard error bars. DOY, Day of Year.

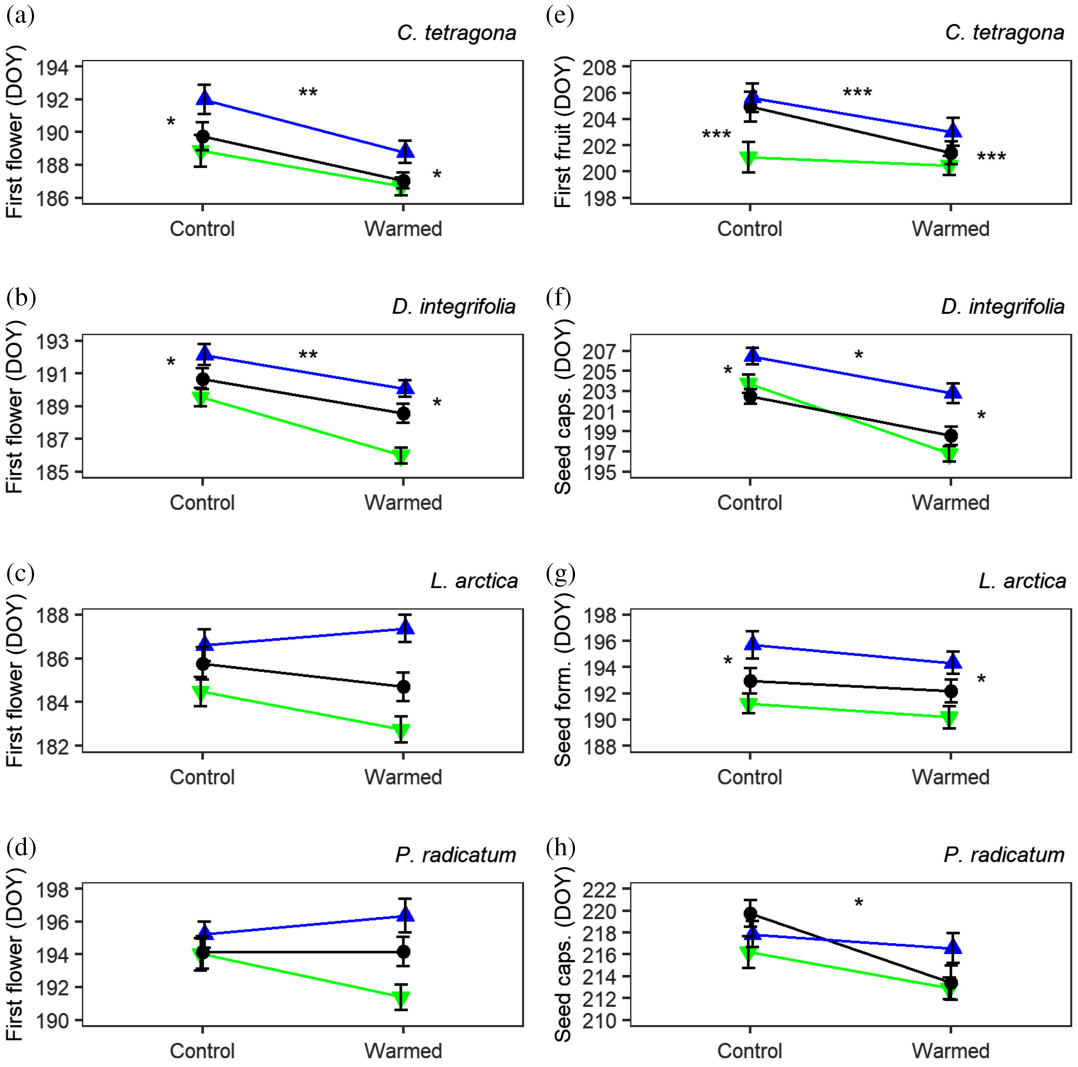


C. tetragona and *D. integrifolia* ($p \leq 0.03$), whereas earlier snowmelt dates were correlated to earlier seed formation in *D. integrifolia* and *P. radicatum* ($p \leq 0.04$).

Growth and reproductive effort

Growth of the two shrub species was increased by experimental warming (Fig. 6 and Table 2) with annual growth increments of 3.6 ± 2.3 mm in warmed vs. 3.3 ± 2.1 mm in control plots in *C. tetragona* ($p = 0.03$; Fig. 6*a*) and taller flower stems (51 ± 24 mm vs. 43 ± 18 mm) in *D. integrifolia* ($p < 0.001$; Fig. 6*b*). In the two herbaceous species, warming did not affect our measurements of growth ($p > 0.1$; Figs. 6*c*, 6*d*). The snow treatments did not influence plant growth in any of the species ($p > 0.3$; Fig. 6). Over the past 21 years, annual growth increments of *C. tetragona* increased by 0.8 mm/decade ($R^2 = 0.33$, $p = 0.02$; Fig. 7*a*)

Fig. 5. Effects of warming and snowmelt treatments (green, snow removal; black, control; blue, snow addition) on average flowering start (*a*–*d*) and seed maturation (*e*–*h*) of *Cassiope tetragona*, *Dryas integrifolia*, *Luzula arctica*, and *Papaver radicatum*. Data are means with standard error bars. Asterisks indicate significantly different treatment means (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). DOY, Day of Year.



under ambient climate conditions. Flower heights of *D. integrifolia* and *L. arctica* also increased by 12.6 mm/decade ($R^2 = 0.27$, $p = 0.07$) and 40.8 mm/decade ($R^2 = 0.73$, $p = 0.001$; Fig. 7*b*, *c*), respectively, whereas growth of *P. radicatum* remained unchanged (–8.5 mm/decade; $R^2 = 0.06$, $p = 0.24$; Fig. 7*d*). There was no significant correlation between plant growth and growing season temperature or snowmelt date.

Flower densities showed species-specific patterns (Fig. 6 and Table 2). In *C. tetragona* and *D. integrifolia*, number of flowers varied strongly from year to year (Fig. 6*e*, *f*). The warming treatment and the snow manipulations did not have consistent effects on this trait in either species. Flower density of *C. tetragona* and *P. radicatum* was increased in experimentally warmed plots ($p = 0.001$, $p = 0.02$; Fig. 6*e*, *h*). For *D. integrifolia* a tendency towards lower flower densities under warming was observed ($p = 0.08$; Fig. 6*f*), whereas in *L. arctica*

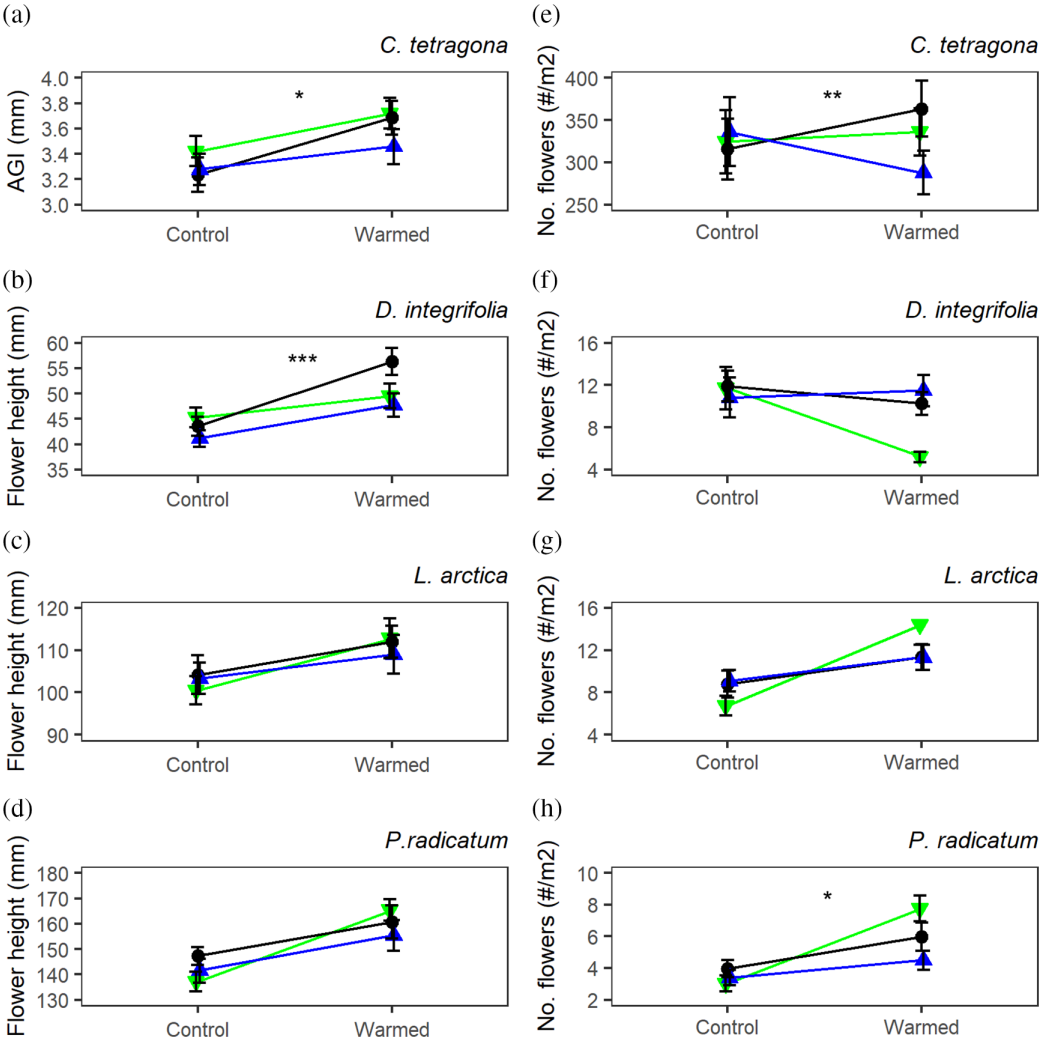
Table 1. Effects of warming and snow manipulation treatments on flowering start and seed maturation of the study species determined by generalized linear mixed effect models.

Response Var.	Species	Treatment	Estimate	SE	*p*
Flowering start	*Cassiope tetragona*	Warming	−2.36	0.79	**0.0027**
		$Snow_{ADD}$	1.63	0.80	**0.0413**
		$Snow_{REM}$	−1.82	0.83	**0.0289**
		Warming × $Snow_{ADD}$	−0.28	1.12	0.8044
		Warming × $Snow_{REM}$	0.50	1.13	0.6582
	Dryas integrifolia	Warming	−1.80	0.65	**0.0056**
		$Snow_{ADD}$	1.58	0.65	**0.0149**
		$Snow_{REM}$	−0.92	0.65	0.1590
		Warming × $Snow_{ADD}$	−0.43	0.92	0.6427
		Warming × $Snow_{REM}$	−1.71	0.93	0.0661
	Luzula arctica	Warming	−1.33	0.79	0.0919
		$Snow_{ADD}$	0.45	0.78	0.5665
		$Snow_{REM}$	−1.51	0.79	0.0556
		Warming × $Snow_{ADD}$	1.66	1.10	0.1339
		Warming × $Snow_{REM}$	0.01	1.12	0.9902
	Papaver radicatum	Warming	−0.05	1.18	0.9658
		$Snow_{ADD}$	1.01	1.11	0.3648
		$Snow_{REM}$	−0.03	1.16	0.9773
		Warming × $Snow_{ADD}$	1.17	1.62	0.4710
		Warming × $Snow_{REM}$	−2.84	1.63	0.0822
Seed maturation	*Cassiope tetragona*	Warming	−3.98	1.08	**<0.001**
		$Snow_{ADD}$	0.47	1.13	0.6766
		$Snow_{REM}$	−3.92	1.18	**<0.001**
		Warming × $Snow_{ADD}$	0.65	1.54	0.6747
		Warming × $Snow_{REM}$	2.56	1.55	0.1000
	Dryas integrifolia	Warming	−3.57	1.53	**0.0198**
		$Snow_{ADD}$	3.53	1.51	**0.0195**
		$Snow_{REM}$	1.30	1.57	0.4052
		Warming × $Snow_{ADD}$	−0.57	2.15	0.7910
		Warming × $Snow_{REM}$	−2.82	2.21	0.2035
	Luzula arctica	Warming	−0.72	0.92	0.4321
		$Snow_{ADD}$	2.22	0.92	**0.0163**
		$Snow_{REM}$	−1.40	0.92	0.1259
		Warming × $Snow_{ADD}$	−1.06	1.30	0.4176
		Warming × $Snow_{REM}$	−0.38	1.30	0.7683
	Papaver radicatum	Warming	−4.27	1.66	**0.0103**
		$Snow_{ADD}$	−1.44	1.58	0.3625
		$Snow_{REM}$	−3.14	1.65	0.0576
		Warming × $Snow_{ADD}$	3.23	2.30	0.1601
		Warming × $Snow_{REM}$	0.87	2.29	0.7055

Note: The full model contained the fixed effects warming, snow addition ($Snow_{ADD}$) and snow removal ($Snow_{REM}$), as well as their interactions. Year and plot were included in the models as random effects. Significant *p*-values are indicated by bold text. For number of observations see Supplementary Table S2[1].

warming had no effect on flower densities ($p = 0.29$; Fig. 6*g*). The main effects of snow treatments did not affect flower densities ($p > 0.2$), but there were interactions between warming and snow treatments in all four species ($p < 0.05$; Fig. 6). In *C. tetragona*, flower densities were reduced under the combination of warming and snow addition as compared with all other treatment combinations ($p = 0.02$; Fig. 6*e*). In *D. integrifolia*, treatment effects were only observed for the combination of warming and snow removal, in which there were significantly fewer flowers ($p < 0.001$; Fig. 6*f*). For the two herbaceous species, the combination of warming and snow removal, but not the other treatment combinations, resulted in greater flower numbers ($p < 0.05$; Fig. 6*g*, *h*). Flower densities of all species

Fig. 6. Effects of warming and snowmelt treatments (green, snow removal; black, control; blue, snow addition) on average growth (*a–d*) and reproductive effort (*e–h*) of *Cassiope tetragona*, *Dryas integrifolia*, *Luzula arctica*, and *Papaver radicatum*. AGI, annual growth increment. No. flowers, flower density measured as number of flower heads per m^2. Data are means with standard error bars. Asterisks indicate significantly different treatment means (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).



remained unchanged over the past 21 years under ambient climate conditions ($p > 0.21$; Supplementary Fig. S4[1]). Similarly, there were no significant correlations between flower densities and growing season temperature or snowmelt dates in any of the species.

Discussion

The results of this long-term experiment combining snow removal, snow addition, and warming in a High Arctic evergreen shrub–heath show that timing of flowering and seed maturation as well as flower production were more strongly influenced by the combined effects of snowmelt timing and warming in the two shrub species than in the two herbaceous species. Experimental warming was effective throughout the growing season

Table 2. Effects of warming and snow manipulation treatments on growth (annual growth increment (AGI) and flower heights) and reproductive effort (flower densities) of the study species determined by generalized linear mixed effect models.

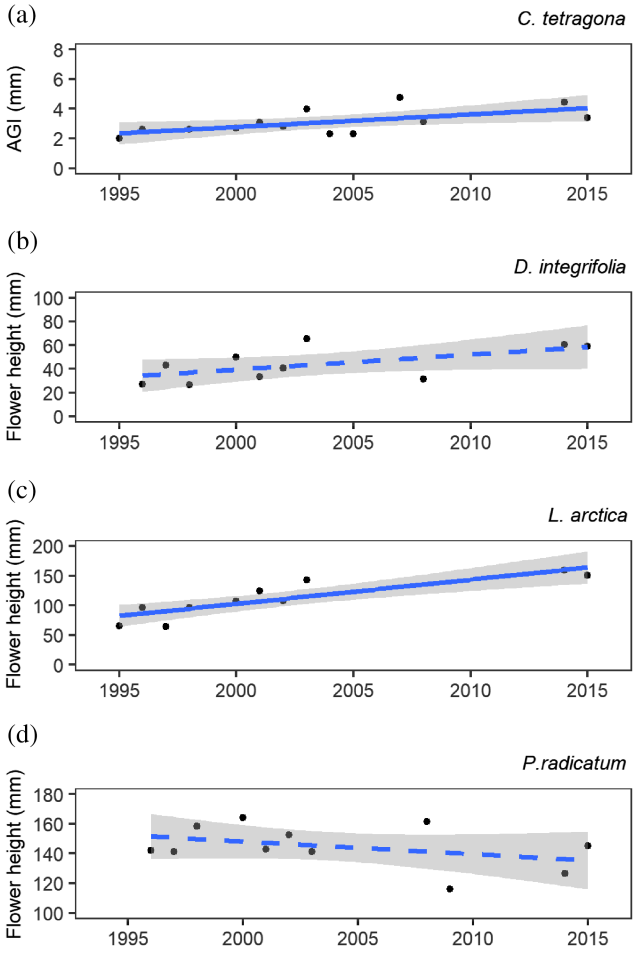
Response Var.	Species	Treatment	Estimate	SE	*p*
AGI	*Cassiope tetragona*	Warming	0.51	0.23	**0.0262**
		$Snow_{ADD}$	0.08	0.23	0.7268
		$Snow_{REM}$	0.23	0.23	0.3049
		Warming × $Snow_{ADD}$	−0.45	0.32	0.1647
		Warming × $Snow_{REM}$	−0.22	0.32	0.5046
Flower heights	*Dryas integrifolia*	Warming	13.93	3.74	<**0.001**
		$Snow_{ADD}$	−2.06	3.71	0.5790
		$Snow_{REM}$	2.53	3.84	0.5103
		Warming × $Snow_{ADD}$	−4.55	5.29	0.3903
		Warming × $Snow_{REM}$	−9.19	5.41	0.0892
	Luzula arctica	Warming	7.56	5.03	0.1330
		$Snow_{ADD}$	−2.03	5.04	0.6870
		$Snow_{REM}$	−1.55	5.02	0.7570
		Warming × $Snow_{ADD}$	0.15	7.12	0.9830
		Warming × $Snow_{REM}$	4.33	7.08	0.5410
	Papaver radicatum	Warming	15.34	10.65	0.1500
		$Snow_{ADD}$	−7.09	10.27	0.4900
		$Snow_{REM}$	−6.28	10.50	0.5500
		Warming × $Snow_{ADD}$	0.20	14.81	0.9890
		Warming × $Snow_{REM}$	11.90	14.73	0.4190
Flower density	*Cassiope tetragona*	Warming	0.33	0.10	**0.0013**
		$Snow_{ADD}$	0.05	0.11	0.6347
		$Snow_{REM}$	0.06	0.11	0.5613
		Warming × $Snow_{ADD}$	−0.33	0.14	**0.0211**
		Warming × $Snow_{REM}$	−0.13	0.14	0.3695
	Dryas integrifolia	Warming	−0.23	0.13	0.0835
		$Snow_{ADD}$	−0.17	0.13	0.2146
		$Snow_{REM}$	−0.17	0.13	0.1971
		Warming × $Snow_{ADD}$	0.31	0.19	0.0934
		Warming × $Snow_{REM}$	−0.54	0.19	**0.0040**
	Luzula arctica	Warming	0.13	0.13	0.2893
		$Snow_{ADD}$	0.08	0.13	0.5301
		$Snow_{REM}$	−0.13	0.13	0.3280
		Warming × $Snow_{ADD}$	−0.11	0.17	0.5200
		Warming × $Snow_{REM}$	0.35	0.17	**0.0457**
	Papaver radicatum	Warming	0.44	0.18	**0.0166**
		$Snow_{ADD}$	−0.14	0.22	0.5149
		$Snow_{REM}$	-0.28	0.22	0.2062
		Warming × $Snow_{ADD}$	−0.16	0.27	0.5510
		Warming × $Snow_{REM}$	0.56	0.27	**0.0393**

Note: The full model contained the fixed effects warming, snow addition ($Snow_{ADD}$) and snow removal ($Snow_{REM}$), as well as their interactions. Year and plot were included in the models as random effects. Significant *p*-values are indicated by bold text. For number of observations compare Supplementary Table S2[1].

resulting in increased shrub growth. The long-term trend of increasing annual growth in the two shrubs and *L. arctica* over the past two decades suggests that warming promoted growth of these tundra species.

Growing season and non-growing season temperatures at Alexandra Fiord increased by approximately 1 °C over the 21-year study period, in line with the long-term temperature trend at the Eureka weather station (Panchen et al. 2021) and the generally increasing temperatures in the Arctic (Meredith et al. 2019). This temperature increase was of the same order as the experimental warming effect of the OTCs of 0.9 °C during the growing period

Fig. 7. Long-term trend of annual growth of *Cassiope tetragona* (*a*), *Dryas integrifolia* (*b*), *Luzula arctica* (*c*), and *Papaver radicatum* (*d*) under ambient temperature and snowmelt conditions over the period of the experiment (1995–2015). Average annual growth increments (AGI) of *C. tetragona* increased by 0.8 mm/decade ($R^2 = 0.33$, $p = 0.02$). Flower heights of *D. integrifolia* and *L. arctica* increased by 12.6 mm/decade ($R^2 = 0.27$, $p = 0.07$) and 40.8 mm/decade ($R^2 = 0.73$, $p = 0.001$), respectively, whereas flower height growth of *P. radicatum* remained unchanged (–8.5 mm/decade; $R^2 = 0.06$, $p = 0.24$). The solid lines show significant linear fits of the data, the dashed lines show non-significant linear fits of the data, and 95% confidence intervals are shaded. Data are means with standard error bars.



(Bjorkman et al. 2015). Total snow accumulation has increased since the 1950s, which is in contrast with other snow measurements in the North American Arctic that found unchanged or decreasing snow cover (Vincent et al. 2015; Bokhorst et al. 2016). There was a slight trend towards earlier snowmelt at the study site since 1995 coinciding with slightly decreasing maximum winter snow depths. However, both trends were not significant. Furthermore, snow depths at the end of May, i.e., shortly before snow manipulations were applied, did not change significantly over the 21-year observation period, indicating consistent, but annually varying, initial conditions for the snow manipulations.

Although there was substantial year-to-year variation in both snow depths and snowmelt dates, the difference in average snowmelt dates between snow removal and addition treatments was only 4.5 days. These small treatment differences in snowmelt timing are in line with findings of a recent review by Rixen et al. (2021), who reported that average differences

between early and late snowmelt were much larger across natural snowmelt gradients (56 days) than in snow manipulation experiments (13.4 days). The small variation in snowmelt dates in our experiment was likely due to the shallow High Arctic snow pack and the timing of the snow manipulations shortly before natural snowmelt. Snow depth at the time the field crew arrived at the site and applied the treatments was usually about 20–30 cm. Although this corresponds to 40%–60% of the maximum snow depth at the site, it limited snow depth differences that could be achieved experimentally. By contrast, snow fence experiments regularly achieve snow depth differences of >1 m, which are unrealistically large in comparison with predicted changes, resulting in snowmelt timing differences of 2–3 weeks (Leffler et al. 2016, Cooper et al. 2019). Nevertheless, the fact that significant snow treatment effects on some traits were found in our experiment indicates that the tundra species are sensitive to even small changes in snowmelt timing.

Unlike snow manipulations, OTCs did not affect snowmelt dates, although average maximum snow depth in the OTCs was 28% greater than in control plots due to the effect of snow trapping (Dorrepaal et al. 2004; Bokhorst et al. 2013). However, increased snowmelt rates through passive warming in the OTCs likely compensated for the additional trapped snow resulting in the small difference in snowmelt dates between OTC and control plots. Thus, the effects of snow treatment and experimental warming on snowmelt dates can be considered independent in our experiment.

Our experimental findings confirm that snowmelt timing is a key driver of phenological events in Arctic tundra species. Earlier snowmelt advanced flowering of the two shrub species, which has been consistently shown by other experimental field manipulations (Wipf and Rixen 2010). Likewise, Høye et al. (2007) found that flowering of *Dryas* sp. closely followed snowmelt timing. Furthermore, later snowmelt delayed flowering initiation in the two shrub species in our experiment. Confirming the importance of snowmelt, Bjorkman et al. (2015) found unchanged flowering phenology despite 1 °C ambient warming over a period of two decades at the same site, which was attributed to unchanged natural snowmelt timing due to increased winter snow depths. Although later snowmelt did not interact with experimental warming in our experiment, the effects of earlier snowmelt on flowering initiation in *D. integrifolia* and *P. radicatum* were slightly more pronounced under elevated temperatures. Thus, flowering phenology of these later flowering species may not only be driven by the timing of snowmelt but also by temperature (Molau 1993, Bjorkman et al. 2015). Later phenological phases usually occur within a fixed time span after snowmelt (Semenchuk et al. 2016) or are controlled by external cues, such as growing degree days (Wipf and Rixen 2010) or changes in light intensity and quality (Biebl 1967; Arft et al. 1999). However, in our study, seed maturation of all species except *P. radicatum* was also affected by snowmelt timing. This finding is in contrast with several other studies showing that only early season phenology of High Arctic plant species is controlled by snowmelt (Bjorkman et al. 2015; Livensperger et al. 2016; Semenchuk et al. 2016).

The observed advanced phenology under experimental warming in the two shrub species is in line with the results of a series of syntheses from the ITEX network demonstrating that temperature is an important driver of plant phenology in tundra ecosystems (Arft et al. 1999; Prevey et al. 2017; Prevey et al. 2019; Collins et al. 2021). This effect may be more important at High Arctic sites with colder summers than at warmer sites at lower latitudes (Prevey et al. 2017; Assmann et al. 2019). Despite substantial ambient warming of 1 °C over the 21-year study period, we did not find long-term shifts in the timing of flowering and seed maturation in the absence of experimental warming and snow treatments. This may be explained by unchanged snowmelt dates due to increasing winter snow depths confirming earlier studies that identified snowmelt timing as more important driver of plant

phenology in High Arctic ecosystems than temperature (Cooper et al. 2011; Bjorkman et al. 2015; Assmann et al. 2019; Bjorkman et al. 2020).

Reproductive effort quantified by flower densities did not reveal consistent patterns across the four study species. Interacting effects between snowmelt and warming seem to drive flower production with snowmelt date being relevant only in warmed but not in control plots. In *D. integrifolia*, earlier snowmelt reduced flower abundances under elevated temperatures. Earlier studies suggested that yearly variation in flower densities may be due to frost damage in areas with early snowmelt (Inouye et al. 2002). Similarly, a study in northeast Greenland, found reduced flower densities in *Dryas octopetala* L. in early snow free plots, which was related to frost events after snowmelt in the year of flowering (Høye et al. 2007). However, severe frost events after application of the snow treatments were rare in our experiment and there was no relation between the occurrence of these events and observed flower densities. The lower flower densities in *D. integrifolia* in warmed plots with earlier snowmelt may also be due to a shift in allocation patterns from reproduction to growth, both above and belowground (Johnstone and Henry 1997; Buchwal et al. 2013; Ropars et al. 2017). However, also late snowmelt can have detrimental effects on reproductive effort, as suggested by the lower flower abundance in *C. tetragona* under experimentally delayed snowmelt and warming. This may be related to insufficient time and resources to fully develop the pre-formed flower buds in this evergreen shrub species due to a shorter growing season (Mallik et al. 2011). However, this could not be confirmed by considering differences in snowmelt timing among years as we did not find significant relations between snowmelt timing and flower abundance. Conversely, positive warming effects on flower production were more pronounced with earlier snowmelt in the two herbaceous species, which may be due to prolonged growing seasons although we did not find any clear relation of flower production with snowmelt timing. Indeed, several studies confirmed enhanced reproductive effort and success in response to warming (Walker et al. 2006; Post et al. 2009), including studies at our experimental site (Klady et al. 2011; Panchen et al. 2021). Nevertheless, we did not find any long-term trend in flower production under ambient warming over the 21 years of observation despite a continuous increase of ambient temperature, which may be related to substantial year-to-year variation, suggesting that the detection of long-term trends will require a longer observation period.

Among year differences of snowmelt timing and average growing season temperature had a substantial influence on phenology traits in some study species. Flowering start in *D. integrifolia* and *L. arctica* closely followed the variation in snowmelt dates with 0.8 days earlier flowering per day of earlier snowmelt. The strong temperature dependence of this early phenological stage is in line with the observed warming response. Remarkably, the phenological response to interannual temperature differences (an advance of 5–7 days/°C warming) was more pronounced than the response to the experimental warming treatment (approximately 2 days/°C). Conversely, plant growth and flower densities were not sensitive to interannual differences in snowmelt timing and growing season temperature, which suggests that growth and flower production in the study species are relatively independent of temperature because of the very effective temperature adaptation of physiological processes such that factors other than temperature are most strongly limiting growth of these species (Chapin 1983). Growth of the study species was not influenced by snowmelt timing, which may, at first, be considered contradictory to the snow–shrub hypothesis. However, the proposed main reason for enhanced shrub growth in this hypothesis—an increase in soil microbial activity due to the insulating effect of a deeper snow cover (Sturm et al. 2005)—would only have a marginal effect in our experiment because snow manipulations were applied shortly before natural snowmelt. However, we cannot rule out that snow trapping in the OTCs may have had a similar effect as snow trapping by shrubs. This could mean

that nutrient availability may have been increased inside the OTCs potentially enhancing plant growth in addition to the direct warming effect. Similar to our experiment, a study in the Alaskan subarctic did not find growth responses to snow manipulations (Wipf 2010). In another study in northern Sweden, experimentally increased snow depths did not affect growth of *Betula nana* L. and *Empetrum hermaphroditum* Lange ex Hagerup, which was explained by relatively small snow depth differences (Keuper et al. 2011). Moreover, individuals with a later growing season start due to delayed snowmelt may be able to compensate for the initial disadvantage with increased growth rates resulting in similar total growth over the complete growing season. Such growth compensation has been described in a study on seven dwarf shrub species in northwestern Finland (Gehrmann et al. 2018).

Under experimental warming, growth of the two shrub species was enhanced, whereas a similar, but non-significant, trend was observed in the two herbaceous species. Similarly, Weijers et al. (2012) observed increased growth of *C. tetragona* under experimental warming and linear temperature–growth relationships in growth chronologies of annual shoot length indicating that growth positively correlated with growing season temperatures. Hudson et al. (2011) measured increased *C. tetragona* and *D. integrifolia* plant heights in response to 16 years of experimental warming in the same mesic heath community at Alexandra Fiord. In a synthesis of tundra warming experiments, Elmendorf et al. (2012*a*) reported greater canopy heights and taller shrubs in response to experimental warming. Furthermore, annual growth increments of *C. tetragona* as well as flower heights of *D. integrifolia* and *L. arctica* increased under ambient warming over the past two decades. Similarly, Elmendorf et al. (2012*b*) reported taller shrubs and taller overall canopy heights in response to ambient warming across the Arctic and plant height was the only variable with a consistent increase over time in a study of community-weighted traits at many tundra sites (Bjorkman et al. 2018). Increased shrub growth over time and in response to experimental warming is in line with the well-described Arctic shrubification (Myers-Smith et al. 2011).

The ability to quantify shifts in phenology may have been affected by the fact that observed phenology shifts of 3–4 days in response to experimental treatments were of similar magnitude as the intervals of phenology observations. Similarly, the observed differences in annual growth increments of *C. tetragona* were on the order of the measurement resolution. By contrast, the growth data and flower densities can be considered robust because they were substantially larger than the measurement resolution. Differences in phenological and quantitative traits between snow treatments and control plots were only found in years in which snow manipulations were applied. Treatment effects disappeared in years when the snow treatments were not applied (Supplementary Figs. S5, S6[1]), which demonstrates that the snow manipulations caused the observed trait differences. This indicates that plants responded to the environmental variation through induced changes in phenotype. This phenotypic plasticity may buffer the effects of rapidly changing environmental conditions such as earlier growing season start, longer growing seasons, or higher average temperatures providing plant species sufficient time to adapt to the altered conditions through evolutionary changes.

Conclusions

Our findings confirm that both snowmelt timing and temperature are important predictors of plant phenology in High Arctic tundra ecosystems. Moreover, these drivers also partly control reproductive effort and growth of tundra plants. The relative importance of the two drivers, however, seems to differ among species, with more pronounced responses in shrubs than in herbaceous species. Accurate predictions of long-term vegetation changes in tundra ecosystems will require extensive and long-term observations of

multiple species at multiple sites to understand the ecological consequences of climate change. Our results underline the importance of complex interactions between temperature and snowmelt timing in driving species-specific plant responses to climate change in the Arctic.

Contributors' statement

GHRH conceived, designed, established and maintained the experiments and the measurements. GHRH and ERF conceived the ideas and designed the methodology for this paper. ERF and GHRH led the acquisition of data. ERF analyzed the data. ERF and GHRH wrote the manuscript.

Data availability statement

All data generated during and (or) analyzed during the current study are available from the corresponding author and the senior author upon reasonable request.

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