NTNU
Norwegian University of Science and Technology

Effects of experimental winter icing and summer warming on high Arctic tundra vascular plants: a comparison of growth forms

Hanne Kristin Haraldsen

NTNU

Norwegian University of
Science and Technology

UNIS

UNIS - The University Centre in Svalbard

cbd

CENTRE FOR BIODIVERSITY DYNAMICS

SVALBARDS
MILJØVERNFOND

Abstract

No other place has experienced such pronounced changes in temperature and precipitation due to climate change, as the terrestrial Arctic. Ecological responses to warmer summers are already well documented, yet the responses to increasing winter temperature and precipitation, are far from understood. Precipitation combined with increased temperature, can result in solid ice layers on the ground, with impacts on plants and animals. Changed climate may cause changes in the plant community, if species respond differently. Understanding responses to changes in the climate and phenomena like rain on snow (ROS) are therefore needed.

I study responses in growth and flowering on plants in Adventdalen (78°N). To simulate the environmental effect of ROS events in winter, ice encasement on the ground was simulated during winter 2015/2016, and established open-top chambers increased the summer temperature (2016) with 0.85 °C and 0.98 °C, then inside control plot. I studied the impact of icing and summer warming treatments through a full factorial randomized block design (n= 36 plots, three blocks) on three key species, the perennial forb *Bistorta vivipara* and the grasses *Poa arctica* and *Alopecurus borealis.* Abundance, flower production, inflorescence height, leaf length, leaf weight, leaf width, surface area and specific leaf area were measured. Except for leaf width in *B. vivipara,* I found no evidence for interactions between icing and warming. Experimental icing increased the abundance of *A. borealis* significantly, had no effect on *P. arctica*, while *B. vivipara* decrease non-significantly. No icing effect was found on inflorescence height, but it decreased the total flower production. During the peak season, *A. borealis* leaves tended to be longer in icing plots, while icing did not affect leaf length and leaf weight of *P. arctica.* Icing had a positive effect on leaf width of *B. vivipara* (in reproductive type in plots with no summer warming), surface area and leaf weight. Summer warming resulted in increased abundance of both grasses, while *B. vivipara* abundance was unaffected. Summer warming also resulted in significant taller inflorescence of *B. vivipara*, greater *P. arctica* mass and showed a tendency for increased total flower production for the three species. This study show large variation among the species in their responses to experimental icing and summer warming. Although responses to icing and warming varied, even small changes in climate influence plant species. Still, climate change will likely be more pronounced in the long term, and affect other trophic levels. Knowledge about responses of key species are important to be able to predict how the ecosystem on Svalbard will respond to future climate change.

Abstract in Norwegian

Arktis er det området som opplever størst endringar i temperatur og nedbør, som følgje av klimaendringar. Økologiske effektar av mildare somrar er allereie eit velkjent forskingstema, medan effektar av auka vinternedbør kombinert med store temperatursvingingar, er ikkje like godt dokumentert. Dette kan føre til isdekke på vegetasjonen, og gje konsekvensar for både plantar og dyr. Dette kan skape endringar i plantesamansetninga, dersom artar blir påverka ulikt. Det er difor viktig å forstå responsar til klimaendringar og fenomen som "rain-on-snow".

Eg undersøkte her vekstresponsar og blomstring hjå plantar i Adventdalen (78°N). Ekstrem ising på grunn av vinterregn vart simulert ved å danne eit solid isdekke på bakken vinteren 2015/2016, og auka sommartemperaturen (2016) med pleksiglas behaldarar ("open- top chambers"). Gjennom eit fullt faktorielt felteksperiment (n= 36 plott, tre blokker), studerte eg kva effekt behandlingane (ising og sommaroppvarming) hadde å seie på veksten og blomsterproduksjonen til tre nøkkelarter, den fleireårige urten *Bistorta vivipara* og grasa *Poa arctica* og *Alopecurus borealis*. Abundans, blomsterproduksjon, blomestandhøgde, bladlengde, bladvekt, bladbredde, overflateareal på blad og spesifikt bladareal vart studert. Bortsett frå bladbredde på *B.* vivipara, fann eg ingen bevis av interaksjon mellom ising og oppvarming. Is-behandlinga auka abundansen til *A. borealis* signifikant, hadde ingen effekt på *P. arctica* og tenderte til å redusere *B. vivipara*. Blomestandhøgda viste ingen signifikant effekt av is-behandlinga, men ising minka antall blomstrar totalt. I høgsesongen viste *A. borealis* tendens for lengre blad av is-behandlinga, medan ingen isingeffekt vart funne på bladlengde og bladvekt hjå *P. arctica*. *B. vivipara* viste positiv effekt av ising på bladbreidde (utan oppvarming), overflateareal og bladvekt. Varmebehandlinga gav auka abundans av *A. borealis* og *P. arctica*, medan *B. vivipara* var upåverka. Varmebehandling gav signifikant høgare blomestand av *B. vivipara*, tyngre *P. arctica* blad og viste ein tendens for totalt auka blomsterproduksjonen av dei tre artane. Resultata frå is-behandlinga og oppvarming viste stor variasjon, men sjølv små klimaendringar påverkar plantearter. Likevel, vil truleg eit endra klimamønster gje større utslag på lang sikt, og potensielt påverke andre komponentar høgare opp i økosystemet. Kunnskap om klimaresponsar hjå plantar er difor viktig for å kunne predikere korleis økosystemet på Svalbard vil respondere på framtidige klimaendringar.

Acknowledgements

Trondheim, June 2017

Hanne Kristin Haraldsen

Table of Contents

Introduction

Global warming causes global changes, such as increased incidence of extreme weather, rise of sea level due to melting of glaciers and heavy precipitation (Mathez, 2009). No other biome is warming as rapidly and strongly as the terrestrial Arctic (AMAP, 2011). Tundra vegetation has already been shown to respond to longer and warmer growing seasons (Callaghan et al., 2011) and even a slight increase in annual summer temperature may have a strong and immediate positive effect on above-ground biomass (van der Wal and Stien, 2014). However, responses can vary among species and growth forms (Callaghan et al., 2011) with different ecosystem functioning and importance, e.g. as food for herbivores. Effects of summer warming are, for many growth forms well documented by summer warming, yet the responses to winter warming are far from understood (Cooper, 2014). Extreme winter warming (warm air temperature for up to a week) has been shown to result in plant damage, such as reduced growth and reduced flowering (Bokhorst et al., 2010). Warm periods with heavy rain-on-snow (ROS) events can also generate thick solid ice layers on the ground (Hansen et al., 2014) with largely unknown effects on tundra plants.

Experimental studies from the sub-Arctic have indicated that, here, icing effects are overall not detrimental for plants (Cooper, 2014). In the high Arctic, however, it was recently shown that an evergreen dwarf- shrub species (*Cassiope tetragona*) not eaten by herbivores was severely affected by experimental icing (Milner et al., 2016). Compared to the controls, plants in icing plots had higher shoot mortality and decreased flower success, while undamaged shoots showed increased growth (Milner et al., 2016). In low productive, bottom- up regulated ecosystem such as the high Arctic, it is important to understand possible changes in plant productivity (van der Wal and Stien, 2014). Studying plant can contribute to a better understanding of climate-induced changes in vegetation (de Groot et al., 1995), and studying winter effects on plants is especially needed to understand arctic ecosystem (Phoenix and Lee, 2004).

Abiotic constraints to plant growth are primarily low air and soil temperature, shallow depth of thaw, low soil nutrient and more drought stress due to higher latitude (Billings, 1987). However, the arctic plants have the ability to grow at temperatures slightly above freezing (Billings, 1987). As both summers are getting warmer and winters rainier, establishing the effects of these climatic drivers on plant performance may contribute to our predictive understanding of future

climate effects on not only the plants themselves, but also their herbivores. One factor in this puzzle will be related to how their key food plants respond to the climate warming during different seasons. On one hand, based on van der Wal and Stien's (2014) study, one might expect an overall positive effect on plant productivity of summer warming, through species clearly respond differently (van der Wal and Stien, 2014). On the other hand, ice encasement, which is increasing in frequency with warmer summers (Hansen et al., 2014), imposes low oxygen conditions on plants and can cause damage as a result of cellular dehydration and acidosis (Preece and Phoenix, 2014). Compared to snow, ice has far less protective insulating capability (Körner, 1999) and repeated freeze/thaw cycles can lead to damaging effects during the growing season (Phoenix and Lee, 2004). If ice- covered plants turn from aerobic respiration to anaerobic respiration, cell death can occur because of accumulation of carbon dioxide and other by- products (Gudleifsson and Bjarnadottir, 2014). In addition, cell membranes may be damaged when the ice melt because of rapid oxidation as tissues are re exposed to air (Crawford, 2014).

Different response time among different ecosystem components and potential interactions between them, makes it hard to predict and understand climate variability and changes (Hansen et al., 2008). The climatic effects can be either direct or indirect, where direct climatic effects cause change without time lags and indirect climatic effect can be delayed (Forchhammer et al., 2008), and the response can be short- or long-term. Short-term changes may not necessary reflect what will happen in the long- term (Hollister et al., 2005). Species may respond in different ways to alterations in growth conditions, and this may cause a change in the composition of the plant communities over time (Ellebjerg et al., 2008). This emphasises the importance of studying different species and growth forms (Ellebjerg et al., 2008).

The aim of this study is to investigate how two potential climate change drivers of plant performance, winter icing and summer warming, affect growth and flowering of key tundra vascular plant species through a field study with a full factorial experimental design in Svalbard. We simulated the environmental effect of winter warming and ROS through ice encasement and summer warming by open- top chambers, and here, I studied several growth responses on three high Arctic tundra plant species *Poa arctica, Alopecurus borealis* and *Bistorta vivipara. P. arctica* and *A. borealis* representing grasses, and *B. vivipara* represent forbs.

Warmer temperature after snow melt is expected to increase plant growth because of improved growing condition (van der Wal and Stien, 2014). Here, I ask whether summer warming increases plant productivity, growth and flowering overall, or do responses to increased temperatures differ among growth forms (forbs and grasses) and species within growth forms (grasses)? I also ask to which extent species respond differently to icing, and whether the combination of icing and warming interact or have a compensatory effect?

Methods

The experiment was run in three mesic sites in the valley Adventdalen close to Longyearbyen, Spitsbergen (Figure 1 A). Here, the climate is cold, but with relatively mild winters compared to the latitude, due to the Golf Stream. In this mesic site, the vegetation is characterized by species such as *Salix polaris*, *Alopecurus borealis, Poa arctica, Luzula confusa, Bistorta vivipara* and several moss species (e.g. *Tomentypnum nitens* and *Sanionia uncinata*).

Experimental design

The sites are located in moss tundra vegetation in Adventdalen (Figure 2 A). The blocks were selected at the end of the summer 2015 (Hovdal et al., 2017). Within each of these three blocks, there was selected twelve 80 cm x 80 cm plots (Figure 1 B). The experimental design is a full factorial randomized block design with controls, with following combinations of treatments: two levels of warming, two levels of icing. Two levels of warming consisted of ambient temperatures and open-top chambers (OTCs) (Arft et al., 1999). The control (C) received no treatment, experimental icing- no warming (I) involved covering the ground with ice during winter 2015/2016, warming- no icing (W) had OTCs on plots during summer, and the combined icing and warming (IW) had ice- encasement during winter 2015/2016 and OTCs during summer. The open-top chambers were placed on the warming plots on May 23rd, after snow melt (estimated as the first day in May (Adapted from Hovdal et al. 2017), to simulate the expected increase in temperature caused by summer climate change. Vertebrate herbivores were excluded from the ambient treatment plots by cages made of metal netting (ca. 1 cm mask size). There was two levels of icing: with and without ground ice. The area within the icing plots was covered by experimental ice from February 2016 (Hovdal et al., 2017). A wooden frame placed on the plot, was filled with water (mixed with snow) from 20 litre cans under cold weather conditions, and the ice encasement became solid ice after two days (Hovdal et al., 2017). This simulated natural icing induced by ROS events in winter. For the combination of summer warming and icing effect, the plots were covered by experimental ice and with open-top chambers on after snow melting. Control had ambient temperature and no icing. This resulted in four treatment combinations. For each treatment combination was replicated three times within each block. 12 plot within the three blocks, gave 36 plots in total. For dividing the plot into sub- squares, a vegetation frame was used (Figure 2 B).
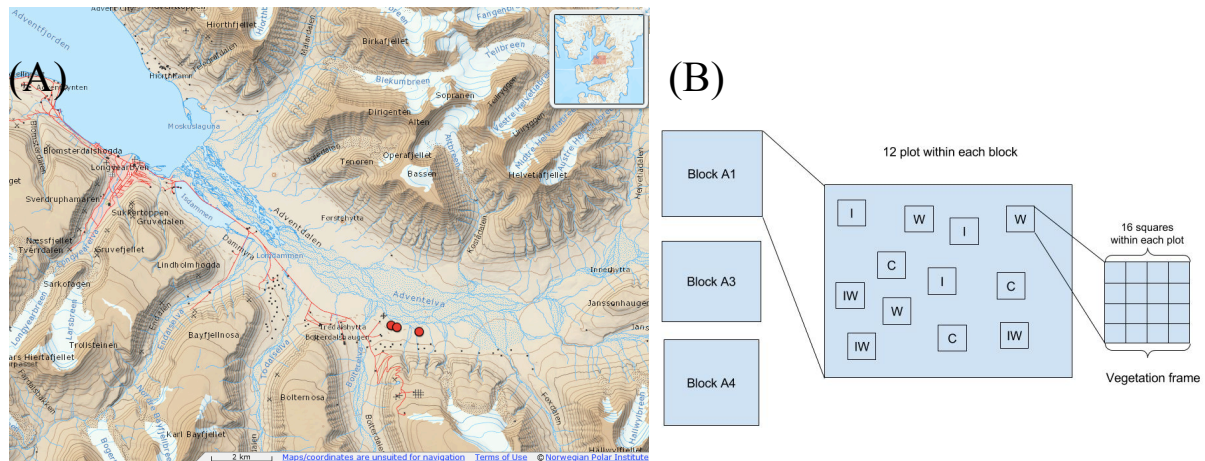
Figure 1. (A) The three red points indicate the location of the three study sites (blocks) in Adventdalen. The map is made in TopoSvalbard @ Norwegian Polar Institute. (B) Schematic overview of the experimental set up. Three blocks with 12 plots were established. C = control plots, I = plots with icing treatment and no warming, W= plots with warming treatment and no icing, IW= plots treated with both experimental icing and summer warming. The vegetation frame used for monitoring and measuring, was divided into 16 sub-squares (Adapted from Hovdal et al. (2017)).

Study species

The study species in this experiment were *Bistorta vivipara, Poa arctica* and *Alopecurus borealis* (Figure 2 C, D, E). The perennial grass *P. arctica* of high importance for the barnacle goose (*Branta leucopsis*) during breeding (Bakker and Loonen, 1998). *P. arctica* is 10- 15 cm tall and with short leaves, and have two modes of clonal growth (Jónsdóttir, 2011). It is a "clonal splitter" through plantlets, and a "clonal integrator" through rhizomes (Jónsdóttir, 2011). Also the grass *A. borealis* and the forb *B. vivipara* are perennial (Rønning, 1996). *A. borealis* is 15- 25 cm tall with rough dark green leaves and grows clonally through rhizomes as *P. arctica* (Rønning, 1996). *B. vivipara* is one of the most widespread arctic- alpine plant species (Marr et al., 2013) and this forb is common in the arctic tundra (Mundra et al., 2016). It has white or pink flowers and ovate lower leaves (Rønning, 1996). The mature state of *B. vivipara* produces inflorescences with both flowers and vegetative bulbils ("clonal splitter") (Jónsdóttir, 2011) and their rhizomes are a key resources for the geese (Anderson et al., 2012). They are 4- 10 cm inflorescences tall. Chicks of Svalbard rock ptarmigan (*Lagopus mutus hyperboreus*) eat more or less only bulbils of *B. vivipara* (Unander et al., 1985).
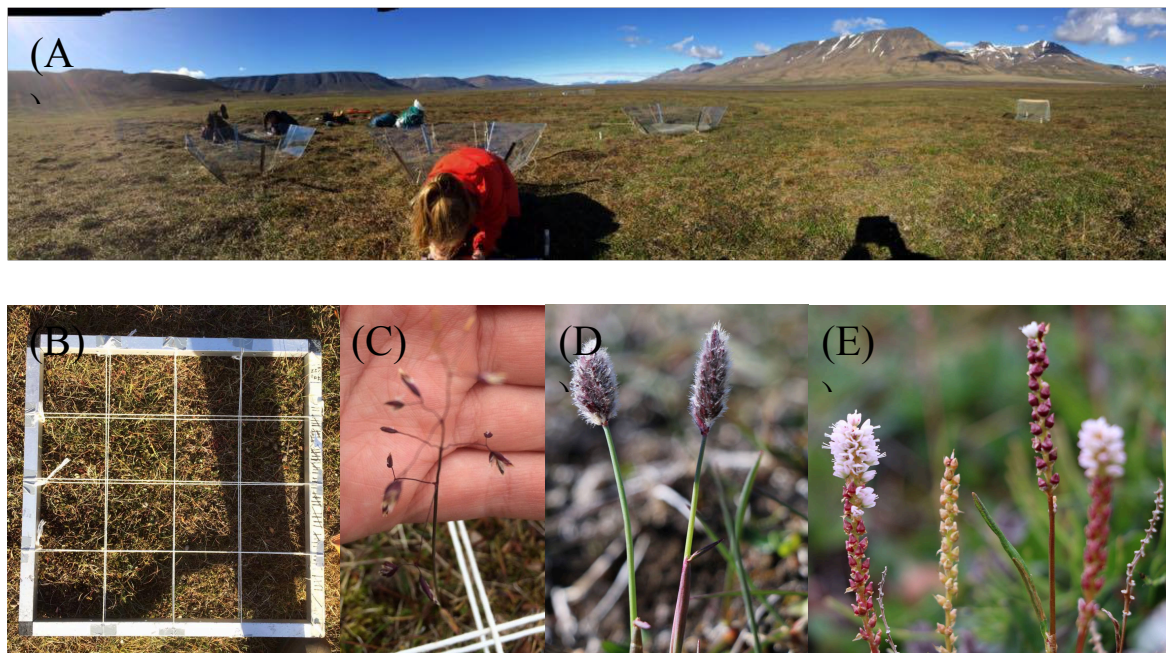
Figure 2. (A) Adventdalen study site with three open-top chambers upside down and fence chamber (to exclude herbivores from control and icing plots) to the right. (B) Vegetation frame. (C) *P. arctica*. (D) *A. borealis* and (E) *B. vivipara* with flowers and bulbils (photo: Katrín Björnsdóttir).

Experimental design

The icing treatment was performed in January- February 2016. The snow depth (mean = 5.1 cm, SD = 1.9 cm) and the thickness of natural occurred ice were measured (mean = 0.9 cm, SD = 1.9 cm) in all plots (from Hovdal et al. (2017)). Before the plots were exposed to water, the snow was removed (Adapted from Hovdal et al. (2017)). In each of the 3 blocks x 6 plots = 18 plots, a 60 x 60 cm wooden box (13 cm high) was placed on the ground and, below freezing, gradually filled with cold water from 20 litre cans, brought to the experimental site by snow mobiles. This was performed on 4th and 5th of February. The ice encasement occurred gradually over two days until the wooden boxes were filled with solid ground-ice (mean = 13.1 cm, SD = 1.1 cm (from Hovdal et al. 2017) (see Milner et al. (2016) for details).

On May 23rd, open-top chambers (Figure 3, C) were placed in 18 of the plots (9 warming and 9 on icing+ warming) (from Hovdal et al. 2017). Open-top chambers allowing a warmer layer of air to develop over the site (Henry and Molau, 1997). The walls are made of Plexiglas's and these chambers are widely used in experimental studies of climate warming effects in plants, both in the Arctic and in alpine regions (Henry and Molau, 1997).

Data collection

For all three species, abundance (number of hits), flower production, inflorescence height, leaf length and leaf weight were measured. For *B. vivipara*, surface area, specific leaf area and leaf width were also measured. From 9th of July till 12th of August 2016, I monitored five observation cycles (in all plots, alternating between the three blocks) for marked shoots or individuals of *P. arctica* and *A. borealis* (Bakker and Loonen, 1998). A vegetation frame (50 x 50 cm), divided into 16 sub- squares, was put on the plot with help of marked sticks in the corners (Bakker and Loonen, 1998). Up to five shoots of each species in each plot were marked in five sub-squares. In each observation cycle, the length of all alive leaves on the marked shoots were measured (in mm) using a yardstick. All leaves on one shoot were given a leaf number. Note that some shoots had already several leaves at the first observation, while other shoots had new leaves in the end of the measuring period. Withered leaves (defined as withered if more than 50 % of the leaf was withered) were not measured, but registered with the same length from the previous observation. One cycle consisted of measuring all the marked shoots in the 36 plots and each observation cycle (round) lasted for 1-3 days, and approximately one week passed between each observation. In total there was five repeated observation cycles with measuring.

All shoots of *P. arctica*, *A. borealis* and *B. vivipara* with flowers were counted on sub-square level on July 13th-15th. On July 30th, the inflorescence height (mm) (measured from the soil surface to the terminal shoot (2008)) of five individuals of all three species was measured in all 36 plot. At the same time, the longest leaf of *B. vivipara* was measured in length (mm) and width (mm) using a yardstick in five sub- squares within the plot. Point intercept analysis of the plant community (number of hits) (Bråthen and Hagberg, 2004), was done in all plots between 2th- 4th of August. In each plot, the point intercept analysis was done lowering a pin (Bråthen and Hagberg, 2004), in each corner of the sub-squares (in a vegetation frame consisting of 25 sub- squares), and the number of each intercept from each of the 9 cross down to the ground surface was recorded.

On 2th-4th of August, leaves from *P. arctica* and *A. borealis* were collected, and on 9th of August, *B. vivipara* leaves were collected. The vegetation frame was put on the plot and the longest leaf

(> 10 mm measured with a yardstick) of *B. vivipara* was collected in five subsquares (other if all leaves < 10 mm). The petioles were clipped off and the leaves were scanned with a grid paper (used as a scale). The leaves were dried in 60 degrees for 24 hours before weighing. Each leaf was weighed separately with a scale. The scanned pictures were used to measure the surface area of each individual leaf by using the image processing program ImageJ (Katabuchi, 2015). Specific leaf area (SLA) was computed by dividing the leaf area by the dry weight (Meziane and Shipley, 1999). Two *P. arctica* shoots and two *A. borealis* shoots were measured and collected, (if possible) close to two plots of each treatments within each block to establish a relationship between leaf length and leaf mass (dry weight). To limit the destructive sampling, two shoots per plot was assumed to be enough to establish this relationship. This was done in one of the block, but fewer measures and collection in the two other blocks (because of less plant presence). The grass leaves collections were outside the vegetation frame, but close enough to include possible treatments effects. The collected leaves were dried in 60 degrees and weighed leaf by leaf with a Mettler Toledo scale.

There was few shoots of grasses outside the vegetation frame, but still within the plot. Thus, only four shoots from each treatment were measured and collected in one of the block (block A1), and even fewer in the two other blocks (block A3 and block A4). For block A3, four plants of *A. borealis* (two shoots from each plot) were measured and collected from each treatment, two *P. arctica* shoots were collected from one icing plot, two shoots from one warming plot and four shoots (two shoots from two plot) from control plots (no collection from combination of icing and warming in A3). In block A4, collection of both species were done in two control plots and one shoot of each species in one IW- plot. Withered grass was not measured, because leaf stop growing when withering. However, grass leaves are produced and wither sequentially during the growing season, and it was necessary to keep track of all leaves that had been produced, i.e. not to exclude the oldest leaves even that they had fully withered and stopped growing. Thus, the last measured length (from previous observation cycle, when the leaf was still not withered) was used in the consecutive observation cycle after its withered.

Statistical analysis

The data were analysed using the statistical software R (Version 1.0.136). To test for treatment effects (icing and warming), I used mixed effect models on the following response variables: abundance, flower production, inflorescence height, leaf length, leaf weight, leaf width, SLA

and leaf area. For count data (flower production and abundance) generalized linear mixed-effect models (glmer) with log link were used, while linear mixed- effects models (lmer) were used on continuous data. The continuous data included inflorescence height of the three species, leaf length on all three species, dried leaf weight on the grasses, leaf width of *B. vivipara*, SLA and leaf area of *B. vivipara*. Environmental variable was standardized (natural ice), in addition to abundance, when it was an explanatory variable for flower production. The package lme4 was used to run mixed effect models and the MuMIn package for R was used to perform backward model selection, starting with the most complex global model. The main effects of icing and warming were always included in all subsets of the global model because I wanted to estimates their effect and uncertainty. The global model included all explanatory variables for that response variables and possible interactions (see Appendix Table A1- table A10). Automated model selection was used with the "dredge" function of the MuMIn package. All models were fitted and parameters estimated using maximum likelihood (ML) methods, using the program lme4 (Burnham and Anderson, 2002). Model selection was based on Akaike Information Criteria corrected for small sample size (AICc) (Burnham and Anderson, 2002). Parameters were estimated based on the best approximating model and fitted with REML (Burnham and Anderson, 2002)), and I used the 'effects' package in R and predicted estimates using the best models (Fox et al., 2016).

For the abundance (number of hits) data, experimental icing, experimental summer warming and natural ice were set as explanatory variables and plot was set as random factor (random intercept effect). For flower production, a model for each species was first made, but because of low sample size (few flowers produced for some species) and since the trends were similar for all species, I also ran a model with all three species together. The explanatory variables in this model were: icing, warming, natural ice and abundance (number of hits). Number of hits is number of hits of each plant from Point frame (standardized). The estimates from the generalized linear mixed- effect models were given on the log link scale, as back transforming is problematic for several reasons (e.g., how to deal with negative estimates and transforming standard error). The 'blmeco' package for R was installed, and according to Bates recommendations, values between 0.75 and 1.4 do not indicate over dispersion (Korner-Nievergelt et al., 2015). The models for abundance of *P. arctica* and *A. borealis* were over dispersed (1.97 and 2.08), while the model for *B. vivipara* was not over dispersed (1.38). For total flower production, there was no evidence of overdispersion (0.92).

For leaf length and leaf weight of *P. arctica* and *A. borealis,* separate models were made. For *P. arctica*, the model for leaf length throughout the season had the following explanatory variables: round (one observation cycle), icing, warming, natural ice and withere, and *A. borealis* had the same explanatory variables except from natural ice. Leaf number nested in plot, nested in blocks was included as random intercept effect. The models for grass leaf length and the models for grass leaf weight (dried) from peak season had experimental icing and warming as explanatory variables with plant number nested in plots nested in blocks as random intercept effects. In addition, models for grass leaf length as a response variable accounting for leaf weight (i.e. leaf length for a given weight) had icing, warming and leaf weight as explanatory variables, while grass leaf weight as a response variable (accounting for leaf length, i.e. leaf weight for a given length), had also icing, warming and leaf length as explanatory variables. The models for leaf weight accounting for leaf length, as a possible effect on leaf shape was investigated, and these models were run to study whether leaves are heavier or lighter for a specific length. Similarly, the models for leaf length accounting for leaf length asks weather leaves are longer or shorter for a specific weight.

For leaf weight of *B. vivipara*, the model had icing and warming as explanatory variables, and plots nested in blocks as random intercept effect. For leaf length of *B. vivipara,* icing, warming and the variable "DevelopmentStage (indicate if the leaf was from *B. vivipara* vegetative or *B. vivipara* reproductive) were explanatory variable. Model for leaf length accounting for leaf width (i.e. leaf length for a given width) had icing, warming and leaf width as explanatory variables. For leaf width, there were interactions between the explanatory variables icing, warming and DevelopmentStage while the model with leaf width accounting for leaf length had icing, warming, leaf length and "Development stage" as explanatory variables without interactions. Model for *B. vivipara* SLA and *B. vivipara* surface area had icing and warming as explanatory variables.

Results

Abundance

For abundance (i.e. number of hits in point intercept analysis) of the three species, experimental icing had a positive effect on abundance of *A. borealis*, no effect on *P. arctica*, while *B. vivipara* tended to get negative affected by experimental icing (p = 0.08) (Table 1 A, Figure 3 a, c, e). Summer warming had a positive effect on both grasses, while there was no effect on *B. vivipara* (Table 1 A, Figure 3 b, d, f).

Flower production and inflorescence height

For flower production, the results from the models with species separated showed increased flower production by summer warming in *P. arctica*, while there was a slight tendency for positive effect in *B. vivipara* and no effect in *A. borealis*. Experimental icing had consistently negative estimates, but only significant in *B. vivipara* (Table 1 B). The result from the model with all species together (species as random intercept effect) suggested that experimental icing had a negative effect in flower production (p < 0.001) (Figure 4 a), while summer warming tended to have a positive effect on flower production (Figure 4 b) For inflorescence height, it was a tendency that warming induced taller plants for all species, but only of *B. vivipara* was significant (p < 0.01) (Table 1 C, Appendix, Figure A1). No evidence for icing effect were found on inflorescence height.

Leaf length

Overall, it was large variation in estimated treatment effects for leaf length among the species. I found no effects of treatment on leaf length of the grasses throughout the season (Figure 5 b, c, e, f. Natural occurred ice has a statistically significant positive effect on *P. arctica* leaf length throughout the season (p < 0.001), (Table 1, D). Withered leaves were statistically shorter than alive leaves (p < 0.001).

At peak season, there was a tendency for a positive effect of icing treatment for *A. borealis* leaf length (p = 0.09), while this effect was not apparent when controlling for leaf weight (Table 1 E). There was no effect of treatments of leaf length of *P. arctica* (Figure 5 g, k), but there was a negative effect of warming when accounting for leaf weight, suggesting that for a given weight, leaves were shorter (Figure 5 j). There was no effect of warming on leaf length of *B. vivipara*, but summer warming tended in longer leaves when accounting for leaf width (not significant) (Table 1 E, Appendix Figure A2). Vegetative leaves of *B. vivipara* were significant longer than reproductive leaves (p < 0.05). The leaf length of *B. vivipara* had no effect of experimental icing (Table 1 E, Appendix Figure A2).

Leaf weight

At peak season, icing had no effect of weight of *P. arctica* leaves, and neither when controlling for leaf length (Table 1 F, Figure 6 a, c). The weight of *A. borealis* leaves was not affected by treatments, neither when accounting for leaf length (Table 1 F, Figure 6 e, f, g, h). Summer warming made the *P. arctica* leaves heavier (p = 0.07) (Figure 6 b), and when accounting for leaf length they were significant heavier than the control (p < 0.01) (Figure 6 b, d). *B. vivipara* leaves had significant heavier leaves in icing plots (p < 0.05), but no effect of warming (Figure 6 i, j).

Leaf width, B. vivipara

For *B. vivipara* leaves total (vegetative and reproductive), there was threeways interaction between icing, warming, and development stages (Table 1 G), suggesting that icing had a positive effect in reproductive leaves but only at ambient temperatures (Table 1, Figure 7 a). When accounting for leaf length, leaf width tended to be negatively affected by warming, suggesting less broad leaves for a given leaf length (p = 0.08) (Figure 7 c).

Specific leaf area and surface area, B. vivipara

For SLA of *B. vivipara*, warming tended to have a negative effect (non- significant), which meant more weight per leaf surface area (Figure 8 a, b). Icing had no effect on SLA of *B. vivipara* (Table 1 H), while icing gave significant larger surface area of *B. vivipara* (p < 0.05) and warming had no effect (Table 1 I, Figure 8 c, d).

Table 1. Mean estimates and standard error for all the best models by the dredge model selection with icing and warming as fixed effects forced to be in all models. The estimates are relative to the control (C) (intercept). Icing is experimental ice treatment, warming is summer warming treatment, natural ice is thickness of natural ice standardized. Wither (more than half of the grass leaf was withered) was a binomial variable (0= still growing, 1= stop growing). DevelopmentStage = indicating if the given leaf was from *B. vivipara* reproductive or *B. vivipara* vegetative. Abundance = number of hits from point frame analysis.

	Response	Species	Model	Mean ± SE	P- values
A	Abundance	*P. arctica*	Intercept (C)	-0.10 ± 0.48	
			Icing	0.08 ± 0.23	p = 0.72
			Warming	0.88 ± 0.25	**p < 0.001**
		A. borealis	Intercept (C)	1.66 ± 0.14	
			Icing	0.43 ± 0.11	**p < 0.001**
			Warming	0.61 ± 0.11	**p < 0.001**
		B. vivipara	Intercept (C)	0.67 ± 0.31	
			Icing	-0.44 ± 0.26	p = 0.08
			Warming	0.06 ± 0.25	p = 0.80
B	Flower production	*P. arctica*	Intercept (C)	0.36 ± 0.16	
			Icing	-0.21 ± 0.21	p = 0.30
			Warming	0.43 ± 0.21	**p < 0.05**
			Abundance	0.18 ± 0.09	**p < 0.05**
		A. borealis	Intercept (C)	0.31 ± 0.22	
			Icing	-0.21 ± 0.27	p = 0.45
			Warming	0.01 ± 0.25	p = 0.98
			Abundance	0.06 ± 0.18	p = 0.62
		B. vivipara	Intercept (C)	-0.46 ± 0.30	
			Icing	-0.55 ± 0.25	**p < 0.05**
			Warming	0.31 ± 0.24	p = 0.20
			Abundance	0.13 ± 0.15	P = 0.37
		All species	Intercept (C)	-1.49 ± 0.50	
			Icing	- 1.03 ± 0.24	**p < 0.001**
			Warming	0.40 ± 0.24	p = 0.09
			Abundance	0.40 ± 0.08	**p < 0.001**
C	Inflorescence height (mm)	*P. arctica*	Intercept (C)	92.79 ± 14.06	
			Icing	11.78 ± 13.71	p = 0.39
			Warming	15.26 ± 13.61	p = 0.26
		A. borealis	Intercept (C)	97.80 ± 11.63	
			Icing	8.91 ± 16.15	p = 0.58
			Warming	19.85 ± 14.62	p = 0.17
		B. vivipara	Intercept (C)	38.30 ± 7.11	
			Icing	2.75 ± 3.98	p = 0.49
			Warming	10.42 ± 3.98	**p < 0.01**
D	Leaf length (mm) (throughout the season)	*P. arctica*	Intercept (C)	29.79 ± 4.17	
			Icing	0.64 ± 2.03	p = 0.75
			Warming	-1.08 ± 2.03	p = 0.59
			Natural ice	3.89 ± 0.95	**p < 0.001**
			Round 2	0.83 ± 1.04	p = 0.42
			Round 3	3.79 ± 1.03	**p < 0.001**
			Round 4	5.20 ± 1.05	**p < 0.001**
			Round 5	5.80 ± 1.07	**p < 0.001**

			Withered	-4.88 ± 1.12	**p < 0.001**
		A. borealis	Intercept (C)	37.50 ± 2.50	
			Icing	1.59 ± 2.76	p = 0.56
			Warming	3.05 ± 2.76	p = 0.27
			Round2	2.72 ± 0.92	**p < 0.01**
			Round3	5.94 ± 0.92	**p < 0.001**
			Round4	8.77 ± 0.93	**p < 0.001**
			Round5	9.65 ± 0.94	**p < 0.001**
			Withered	-12.33 ± 1.11	**p < 0.001**
E	Leaf length (mm) (peak)	*P. arctica*	Intercept (C)	31.79 ± 3.44	
			Icing	-1.47 ± 2.89	p = 0.61
			Warming	-1.62 ± 3.08	p = 0.60
	Leaf length (mm) (peak) accounting for leaf weight	*P. arctica*	Intercept (C)	21.04 ± 2.35	
			Icing	-0.44 ± 2.24	p = 0.84
			Warming	-5.18 ± 2.40	**p < 0.05**
			Leaf weight	4.66 ± 0.59	**p < 0.001**
	Leaf length (mm) (peak)	*A. borealis*	Intercept (C)	45.86 ± 4.12	
			Icing	8.27 ± 4.86	p = 0.09
			Warming	-1.82 ± 4.86	p = 0.71
	Leaf length (mm) (peak) accounting for leaf weight	*A. borealis*	Intercept (C)	16.67 ± 3.89	
			Icing	3.12 ± 4.29	p = 0.46
			Warming	1.15 ± 4.26	p = 0.79
			Leaf weight	5.02 ± 0.31	**p < 0.001**
	Leaf length (mm)	*B. vivipara*	Intercept (C)	16.52 ± 1.78	
			Icing	0.10 ± 0.91	p = 0.91
			Warming	1.03 ± 0.91	p = 0.26
			Bistortaveg	1.02 ± 0.50	**p < 0.05**
	Leaf length (mm) accounting for leaf width	*B. vivipara*	Intercept (C)	12.85 ± 1.71	
			Icing	0.005 ± 0.88	p = 0.99
			Warming	1.33 ± 0.88	p = 0.13
			Leaf width	0.74 ± 0.12	**p < 0.001**
F	Leaf weight (mg)	*P. arctica*	Intercept (C)	2.32 ± 0.78	
			Icing	-0.17 ± 0.43	p = 0.70
			Warming	0.83 ± 0.46	p = 0.07
	Leaf weight (mg) accounting for leaf length	*P. arctica*	Intercept (C)	-0.35 ± 0.64	
			Icing	-0.04 ± 0.33	p = 0.90
			Warming	0.98 ± 0.36	**p < 0.01**
			Leaf length	0.08 ± 0.01	**p < 0.001**
	Leaf weight (mg)	*A. borealis*	Intercept (C)	5.68 ± 0.73	
			Icing	1.00 ± 0.86	p = 0.25
			Warming	-0.46 ± 0.86	p = 0.59
	Leaf weight (mg) accounting for leaf length	*A. borealis*	Intercept (C)	-1.04 ± 0.74	
			Icing	-0.21 ± 0.76	p = 0.78
			Warming	-0.36 ± 0.75	p = 0.63
			Leaf length	0.15 ± 0.01	**p < 0.001**
	Leaf weight (mg)	*B. vivipara*	Intercept (C)	4.22 ± 0.76	
			Icing	1.10 ± 0.50	**p < 0.05**
			Warming	0.57 ± 0.50	p = 0.25
G	Leaf width (mm)	*B. vivipara*	Intercept (C)	4.22 ± 0.45	
			Icing	1.47 ± 0.52	**p < 0.01**
			Warming	0.40 ± 0.49	p = 0.42
			DevelopmentStage	2.27 ± 0.42	**p < 0.001**
			Icing:Warming	-2.03 ± 0.70	**p < 0.01**
			Icing: DevelopmentStage	-1.66 ± 0.61	**p < 0.01**

			Warming:DevelopmentStage	-0.66 ± 0.58	p = 0.25
			Icing:Warming:DevelopmentStage	2.28 ± 0.83	**p < 0.01**
	Leaf width (mm) accounting for leaf length	*B. vivipara*	Intercept (C)	2.59 ± 0.42	
			Icing	0.11 ± 0.27	p = 0.68
			Warming	-0.48 ± 0.29	p = 0.08
			DevelopmentStage	1.57 ± 0.20	**p < 0.001**
			Leaf length	0.13 ± 0.02	**p < 0.001**
H	SLA (mm^2/mg)	*B. vivipara*	Intercept (C)	13.91 ± 0.83	
			Icing	-0.38 ± 0.65	p = 0.56
			Warming	-1.07 ± 0.65	p = 0.10
I	Surface area (mm^2)	*B. vivipara*	Intercept (C)	56.82 ± 12.21	
			Icing	14.64 ± 7.09	**p < 0.05**
			Warming	3.77 ± 7.05	p = 0.59

Abundance
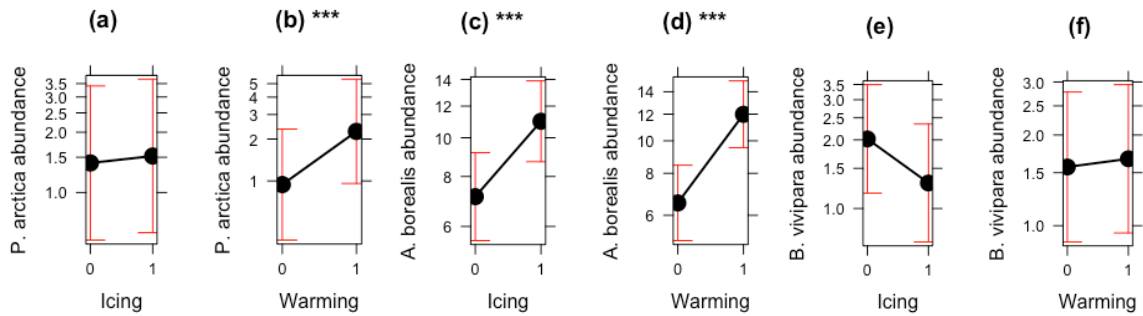
Figure 3. Effect plots of effect of icing (0= not icing, 1= icing treatment) and warming (0= not warming, 1 = warming treatment) on abundance (number of hits) of *P. arctica* (a, b), *A. borealis* (c, d) and *B. vivipara* (e, f) in icing treatment (a, c, e) and warming treatment (b, d, f) in August 2016. Significant predicted estimates have subheadings with ***, when p < 0.001.

Flower production
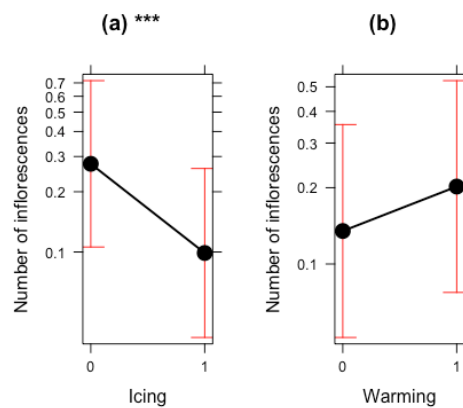
Figure 4. Effect plots of icing (0= not icing, 1= icing treatment) on flower production of total shoots of *P. arctica*, *A. borealis* and *B. vivipara* with flowers (a), and effect plot of warming (0= not warming, 1 = warming treatment) on flower production of total shoots of *P. arctica*, *A. borealis* and *B. vivipara* with flowers (b) (p = 0.09) in July 2016. Significant predicted estimate has subheading with ***, when p < 0.001.

Leaf length
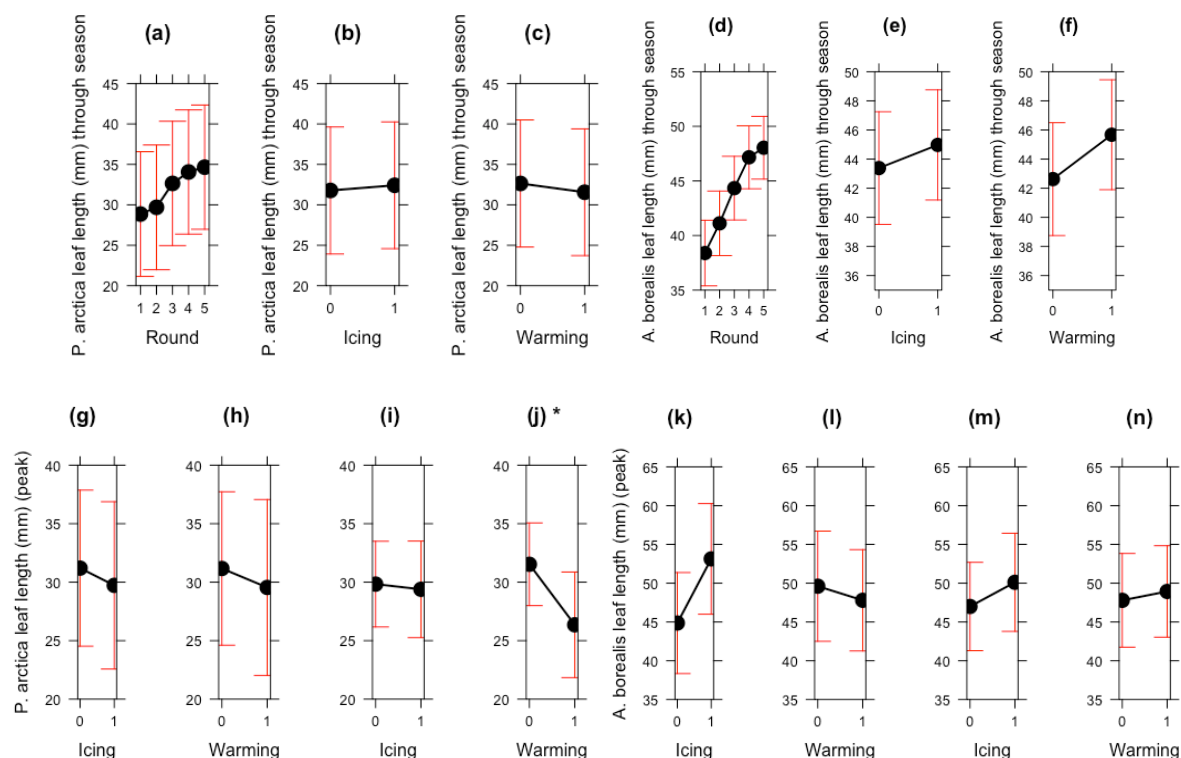
Figure 5. Effect plots of experimental icing (0= not icing, 1= icing treatment) (b, e) and summer warming (0= not warming, 1 = warming treatment) (c, f) on leaf length (mm) of *P. arctica* and *A. borealis* throughout the season. Effect plot of the growth of the leaf length throughout the season from observation cycle 1 (round 1) in July till observation cycle 5 (round 5) in August (a, d). Icing effect on leaf length of *P. arctica* (b) and of *A. borealis* (e), and warming effect on leaf length of *P. arctica* (c) and *A. borealis* (f) throughout the season. Effect plot of experimental icing on *P. arctica* (g), and when accounting for leaf weight (i), and effect plot of summer warming on *P. arctica* (h), and when accounting for leaf weight (j). Effect plot of experimental icing on *A. borealis* (k), and when accounting for leaf weight (m). Effect plot of summer warming on *A. borealis* (l), and when accounting for leaf weight (m). Significant predicted estimate has subheading with *, when p < 0.05.

Leaf weight
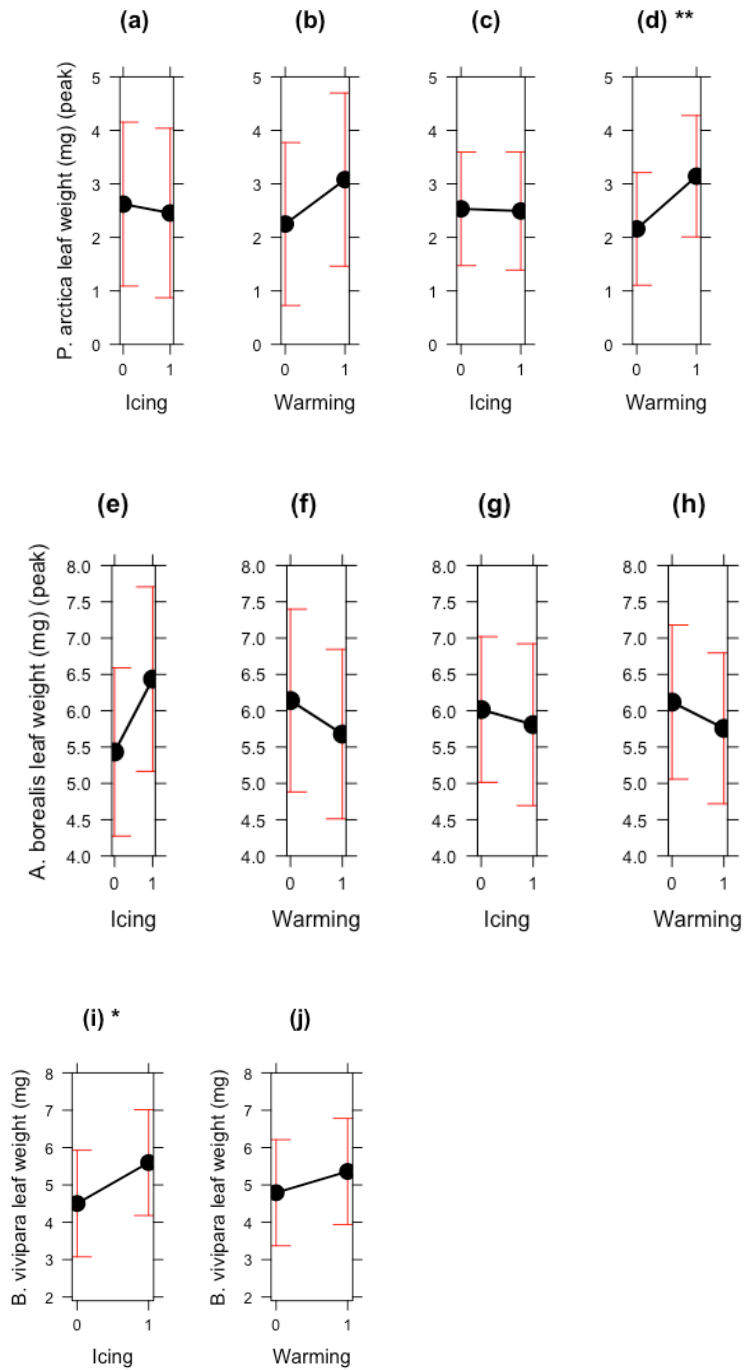
Figure 6. Effect plots of experimental icing (a, e, i) and summer warming (b, f, j) on leaf weight (mg per leaf) of *P. arctica*, *A. borealis* and *B. vivipara* at peak season. Effect plot of experimental icing (c, g) and summer warming (d, h) on leaf weight of *P. arctica* and *A. borealis*, when accounting for leaf length. Significant predicted estimates have subheadings with **, when p < 0.01, and *, when p < 0.05.

Leaf width

(a)
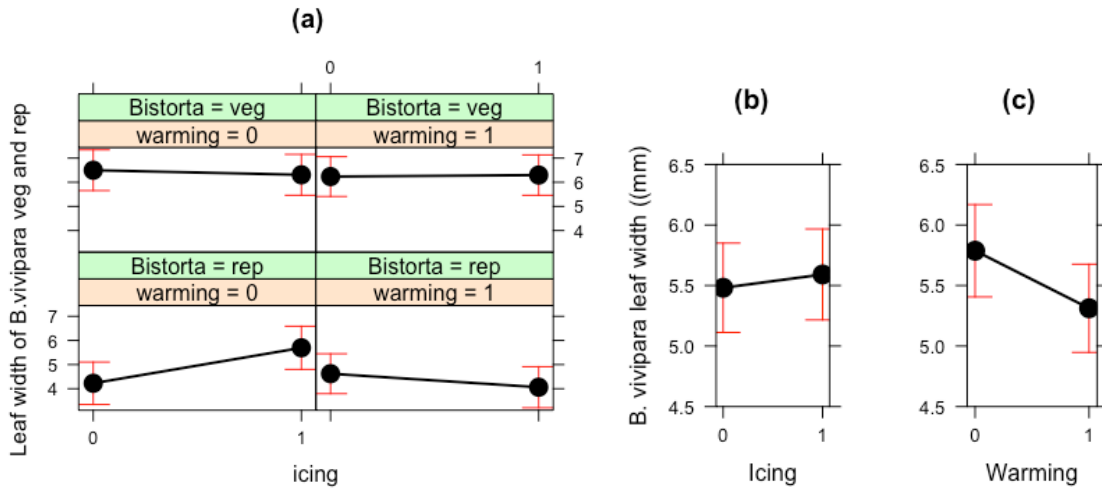
Figure 7. Effect plot of experimental icing and summer warming on leaf width (mm per leaf) responses of *B. vivipara* vegetative (veg) and reproductive (rep) (a), and all effect plots of icing (b) and warming (c) (p= 0.08) on leaf width of *B. vivipara,* when accounting for leaf length. For significance in "(a)", see Table 1, E.

Specific leaf area and surface area
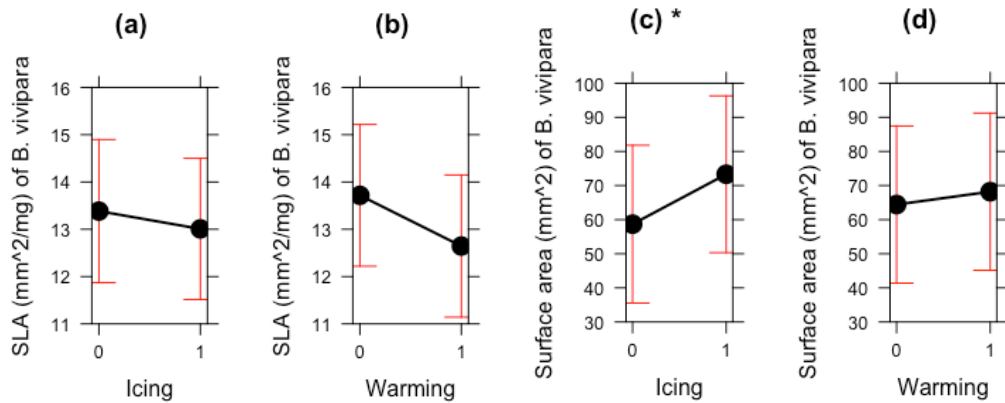
Figure 8. Effect plots of experimental icing (a) and summer warming (b) on specific leaf area (mm^2/mg per leaf) of *B. vivipara*, and effect plot of experimental icing (c) and summer warming (d) on surface area (mm^2 per leaf) of *B. vivipara*. Significant predicted estimate has subheading with *, when p < 0.05.

Discussion

In the present study, the effects of experimental winter icing and summer warming on growth and flowering of three high Arctic key vascular plant species were investigated. The winter icing was simulated through the artificial addition of solid ice, and the summer warming by open- top chambers. This is among the first studies on winter icing on high Arctic plants, implemented in their natural ecosystem. The results from this short- term experiment indicate that the impact of icing and increased temperature on growth, were species- specific. Responses such as abundance of *P. arctica*, inflorescence height of all three species, leaf length of *P. arctica* and *B. vivipara*, and leaf mass of the grasses, showed no effect of icing. *A. borealis* seemed to have higher tolerance to winter icing than *P. arctica* and took advantage of it in e.g. abundance, and tended for longer leaves during peak season. Icing had a positive effect on leaf weight, leaf width of reproductive *B. vivipara* (but only at ambient temperatures) and surface area of *B. vivipara*, but tended to reduce the abundance of *B. vivipara*. Warming resulted in both increased or decreased growth compared to the control (i.e. ambient temperature and no icing). Increased temperature seemed to provide better growth conditions for e.g. grass abundance, and increased inflorescence height of *B. vivipara*. Nevertheless, increased temperature may have led to drier growth conditions as indicated by tendencies for e.g. shorter *P. arctica* leaf in peak season and tended for narrower *B. vivipara* leaf when accounting for leaf length. Except from *B. vivipara* leaf width, I found no effect for the combination of icing and warming.

Because I wanted to test the effects/uncertainties of experimental icing and summer warming, model selection with experimental icing and summer warming were forced into the 'best' model, and the best model for each response variable showed possible tendencies of the treatments. In total, both treatments showed more positive mean estimates with an effect, than negative mean estimates with an effect. This indicate a tendency of some treatments effects on plants growth and flowering. However, most of the mean estimates showed no effect of the treatments.

Summer warming increased the abundance of the grasses significantly, but no effect on the perennial forb *B. vivipara*. This suggests that the short term change by increased warming had an impact on different growth form, and partly match the long term (up to 85 years) change reported by Kapfer and Grytnes (2017) in 2009. They found that several grass species on Svalbard (e.g., *A. borealis*) had increased in occurrence frequencies since three earlier studies from the 20th century (Lid, 1967, Hadač, 1946, Rønning, 1996), while several species of forbs had decreased in frequency. However, our results for *B. vivipara* had several positive estimates due to summer warming. Chapin et al. (1995) found a great reduction in species richness by temperature and nutrient treatment in Alaska over a nine- year period. Rare species decreased, while the four most abundant species in that area increased (Chapin et al., 1995). This suggests potential changes in vegetation composition due to environmental conditions.

The results with positive effect for inflorescence height of *B. vivipara*, can be explained by the early snowmelt. Based on the tendencies for taller plants (inflorescences) and in response to increased summer temperature, we may expect taller plant among some species in the high Arctic in years with early snowmelt. Although summer warming affected some variables on *P. arctica* and *A. borealis* equally, they did not always show the same tendencies in length and weight, despite the same growth form and similar traits. This match the result from Chapin et al. (1995), where two graminoids had contrasting responses. The aim of measuring the grass leaves throughout the season was to assess the cumulative leave production, but there was no treatment effect to detect after one summer. Nevertheless, the leaf size of arctic graminoids may increase strongly with warming (Arft et al., 1999). The different response due to increased temperature, could indicate that *A. borealis* did not respond to warming, while *P. arctica* increased in biomass through heavier leaves. This illustrates the importance of not generalizing for growth forms based on results from one or a few species. Semenchuk et al. (2016) emphasized the importance to not assume that species sharing common traits in phenology, will react similarly to the timing of snowmelt, based on two species. For the perennial forb *B. vivipara*, the results for specific leaf area indicated that the leaves tended to became shorter and thicker with increased temperature. Hudson et al. (2011) showed that larger leaf size and taller plants were the most common long- term responses due to long- term warming by OTCs on several tundra plant in Canada, but with varied responses at different sites. Based on this, and the result for varying responses among the three study species, increased temperature might not

be beneficial for growth and inflorescence in all species. This may suggest a changed plant composition with a predicted warmer climate.

Based on few earlier studies on winter icing effects on vegetation, it was uncertain what to expect. In addition, the experimental ice caused only a slight delay in melting time (Hovdal et al., 2017). For species abundance, the three species responded differently to winter icing treatment. *A. borealis* appeared to take advantage of the disturbance and increased considerably in abundance (0.43 ± 0.11), *P. arctica* was unaffected, while number of *B. vivipara* tended to decrease with experimental icing (-0.44 ± 0.26). However, experimental icing decreased the flower production overall, which is in agreement with the results from a study in Adventdalen where delayed start of growing season decreased the number of flowers (Cooper et al., 2011). According to Milner et al. (2016), plants in icing plots had lower flower success than the control. The same study showed that plants with many flowers invested less in shoot growth (Milner et al., 2016). My results may indicate the opposite case; that plants with few flowers invested more in shoot growth.

Overall for leaf length, experimental icing showed no effect , except from a tendency for longer *A. borealis* leaf during peak season. For *A. borealis*, this may possibly indicate a delayed growth due to the icing. This suggests that *A. borealis* increased their biomass due to icing, while *P. arctica* was unaffected. No difference in *B. vivipara* leaf length in icing plots compared to the control may be explained by the species development character. Up to four years are needed for each leaf to develop, and to progress the whole inflorescence process (Diggle, 1997). Naturally occurring ice was only included in the best model for *P. arctica* throughout the season. With the amount of naturally occurring ice, its low impact was unexpected. Natural occurred ice may have been a confounding effect. Like melted snow, melted ice give the vegetation supply of water and transport nutrient (Elberling et al., 2008). This might give good growth conditions and possible transported nutrient in the melted water. The icing had a positive effect on leaf width of *B. vivipara* reproductive, but no effect on leaf length of *B. vivipara* vegetative. The model of *B. vivipara* leaf width was the only model with threeways interaction between icing, warming and growth form included in the best model, and the combination of the treatments gave significant bigger surface area. In the model for leaf length of *B. vivipara*, accounting for leaf width there was no change in the shape of the leaf.

Natural ice increased the leaf length of *P. arctica*. The different combination of treatments at peak season had varied results among the three species. Summer warming resulted in significantly shorter *P. arctica* leaves when accounting for leaf mass, experimental icing had a tendency for longer *A. borealis* leaves, while *B. vivipara* did not have any significant changes in leaf length in response to warming or icing. Increased temperature resulted also in heavier *P. arctica* leaves, while increased temperature had no effect on leaf mass of *A. borealis*. In contrast to these varied results, found Arft et al. (1999) in their meta- analysis on tundra plants, small effects of experimental warming on forbs and graminoids.

The large uncertainty in the estimates for leaf length and leaf weight of the two grasses from peak season may be strongly related to the small sample size. Earlier studies (Ellebjerg et al., 2008, Callaghan et al., 2011) have shown variations in responses among different growth forms and growth organs. In addition, it was large variations within species, and especially the perennial herb *B. vivipara* showed both positive and negative effects by experimental icing. However, the icing had few significant effects. Furthermore, responses to environmental changes may be slow and shown later. In addition, there are trade- offs between growth or reproduction, and species have different life- history strategies (Jónsdóttir, 2011). I expected that grasses would respond more similar compared to the forb, which was the case for some parameters, but also an effect on only one of the species, in e.g. leaf length and leaf weight in peak season. This suggest a species- specific response due to environmental changes. However, the results from this study must be interpreted carefully for several reasons. Firstly, this study included only three species, two grasses and one perennial forb, with large variation in predicted estimates and many estimates with no effect. Arctic plants show large year to year variation due to snow depth (Mallik et al., 2011), and the early snowmelt in spring 2016 and the ice encasement caused only a small delay. Investigation over a longer period will increase the quality of the experiment. In addition, the warming treatment had only a small temperature rises due to cloudy weather, with a temperature rises inside the warming plots between 0.85 °C and 0.98 °C higher than inside control plots. With a sunny summer, it would probably have been more significant impact of the warming parameters. In addition, it is likely that an early snowmelt in 2016 caused an earlier peak season than my measurement suggested. Since the grass leaf already started to shrink and wither around turn of July and beginning of August. For

the grass measurements throughout the season, a longer period and continued measurements on the withered leaves would have been more precise. To increase the power of the experiment, more experimental units (bigger sample size) and several species should be included, and due to low sample size, uncertain estimates and large standard errors, one should be cautious to make conclusive statements.

In this thesis, I have analysed each variable separately for each species (except from flower count where a pooled model was made because of similar tendency for icing effect). I could have used two alternative methods. First, I could have made a new variable for e.g. growth, based on two or more leaf variables, and then have done the statistical analysis on that new variable. Second, I could have analysed the variables separately (as I did), but with adding related variables as explanatory variables. With these options it might have been easier to compare with other studies and the sample size would increase. However, the risk of getting significant results by chance would for some variables, been higher.

This study suggests that responses of growth parameters and flowering are not grouped to growth- form, but are species- specific. Summer warming showed tendency for increasing flower production and different part of each species. Nevertheless, leaf length, when accounting for leaf weight of *P. arctica* in peak season, got significant shorter with increased temperature. Experimental icing had, as expected, a negative effect for some variables of all three species, but *A. borealis* and *B. vivipara* seemed also to take advantage of the icing disturbance. *A. borealis* increased in abundance and had a tendency for longer leaves in peak season, and *B. vivipara* got heavier leaves, wider reproductive leaves and larger surface area in icing plots. With varying responses to a changed environment, we expect changes in the plant community composition. Species may increase their abundance because of good adaptability, while other species may over time disappear (Kapfer and Grytnes, 2017). To be able to predict and understand how these regions will respond to environmental change, knowledge about how the vegetation will respond is crucial (Harding et al., 2001, Hudson et al., 2011). This requires an in- depth and long- term investigation, on several species, several parameters and over a longer period. Species may be outcompeted by others, if reduced growth and less production performance are consequences of changed environment (Mallik et al., 2011). Other species will also be affected, since species in a biome such as the high Arctic are highly dependent on each

other. With limited resources in an ecosystem like this, changed climate will hence likely cause community changes. This experiment has clearly shown that even very small changes in the climate, through icing and summer warming, have a large impact on key tundra vascular plant species. Furthermore, these responses show that the community level effects of climate change and associated phenomena, such as ROS events, will be a big challenge in the future.

References

2008. Effects of Growth Regulator Application on Growth, Flower, Oil Yield, and Quality of Clary Sage (Salvia sclarea L.). *Journal of Herbs, Spices & Medicinal Plants,* 14**,** 31.

AMAP 2011. Snow, water, ice and permafrost in the Arctic (SWIPA): climate change and the cryosphere. Oslo.

Anderson, H. B., Godfrey, T. G., Woodin, S. J. & Van Der Wal, R. 2012. Finding food in a highly seasonal landscape: where and how pink footed geese Anser brachyrhynchus forage during the Arctic spring. *Journal of Avian Biology,* 43**,** 415-422.

Arft, A., Walker, M., Gurevitch, J., Alatalo, J., Bret-Harte, M., Dale, M., Diemer, M., Gugerli, F., Henry, G., Jones, M., Hollister, R. D., Jónsdóttir, I., Laine, K., Lévesque, E., Marion, U., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., Robinson, C., Starr, G., Stenström, A., Stenström, M., Totland, Ø., Turner, L., Walker, L., Webber, P. J., Welker, J. M. & Wookey, P. A. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological monographs,* 69**,** 491-511.

Bakker, C. & Loonen, M. J. J. E. 1998. The influence of goose grazing on the growth of Poa arctica: overestimation of overcompensation. *Oikos,* 82**,** 459-466.

Billings, W. D. 1987. Constraints to Plant Growth, Reproduction, and Establishment in Arctic Environments. *Arctic and Alpine Research,* 19**,** 357-365.

Bokhorst, S., Bjerke, J. W., Davey, M. P., Taulavuori, K., Taulavuori, E., Laine, K., Callaghan, T. V. & Phoenix, G. K. 2010. Impacts of extreme winter warming events on plant physiology in a sub-Arctic heath community. *Physiologia Plantarum,* 140**,** 128-140.

Bråthen, K. A. & Hagberg, O. 2004. More efficient estimation of plant biomass. *Journal of Vegetation Science,* 15**,** 653-660.

Burnham, K., P. & Anderson, D. R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*, Springer Science & Business Media.

Callaghan, T. V., Tweedie, C. E., Åkerman, J., Andrews, C., Bergstedt, J., Butler, M. G., Christensen, T. R., Cooley, D., Dahlberg, U., Danby, R. K., Daniëls, F. J. A., De Molenaar, J. G., Dick, J., Mortensen, C. E., Ebert-May, D., Emanuelsson, U., Eriksson, H., Hedenäs, H., Henry, G. H. R., Hik, D. S., Hobbie, J. E., Jantze, E. J., Jaspers, C., Johansson, C., Johansson, M., Johnson, D. R., Johnstone, J. F., Jonasson, C., Kennedy, C., Kenney, A. J., Keuper, F., Koh, S., Krebs, C. J., Lantuit, H., Lara, M. J., Lin, D., Lougheed, V. L., Madsen, J., Matveyeva, N., Mcewen, D. C., Myers-Smith, I. H., Narozhniy, Y. K., Olsson, H., Pohjola, V. A., Price, L. W., Rigét, F., Rundqvist, S., Sandström, A., Tamstorf, M., Van Bogaert, R., Villarreal, S., Webber, P. J. & Zemtsov, V. A. 2011. Multi-Decadal Changes in Tundra Environments and Ecosystems: Synthesis of the International Polar Year-Back to the Future Project (IPY-BTF). *Ambio,* 40**,** 705-716.

Chapin, F. I., Shaver, G., Giblin, A., K., N. & Laundre, J. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology,* 76**,** 694-711.

Cooper, E. J. 2014. Warmer Shorter Winters Disrupt Arctic Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics,* 45**,** 271-295.

Cooper, E. J., Dullinger, S. & Semenchuk, P. 2011. Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. *Plant Science,* 180**,** 157-167.

Crawford, R. M. M. 2014. *Tundra- Taiga biology: human, plant and animal survival in the Arctic. ,* Oxford, U.K. , Oxford University press.

de Groot, R. S., Ketner, P. & Ovaa, A. H. 1995. Selection and use of bio- indicators to assess the possible effects of climate change in Europe. *Journal of Biogeography,* 22**,** 935-943.

Diggle, P. 1997. Extreme prefornation in alpine Polygonum viviparum: an architectural and developmental analysis. *American Journal of Botany,* **84,** 156.

Elberling, B., Tamstorf, M. P., Michelsen, A., Arndal, M. F., Sigsgaard, C., Illeris, L., Bay, C., Hansen, B. U., Christensen, T. R., Hansen, E. S., Jakobsen, B. H. & Beyens, L. 2008. Soil and Plant Community-Characteristics and Dynamics at Zackenberg. *Advances in Ecological Research.* Academic Press.

Ellebjerg, S. M., Tamstorf, M. P., Illeris, L., Michelsen, A. & Hansen, B. U. 2008. Inter-Annual Variability and Controls of Plant Phenology and Productivity at Zackenberg. *Advances in Ecological Research.* Academic Press.

Forchhammer, M. C., Schmidt, N. M., Høye, T. T., Berg, T. B., Hendrichsen, D. K. & Post, E. 2008. Population Dynamical Responses to Climate Change. *Advances in Ecological Research.* Academic Press.

Fox, J., Weisberg, S., Friendly, M., Hong, J., Andersen, R., Firth, D. & Taylor, S. 2016. Effect Displays for Linear, Generalized Linear, and Other Models.

Gudleifsson, B. E. & Bjarnadottir, B. 2014. Estimating ice encasement tolerance of herbage plants. *Methods Mol Biol,* 1166**,** 225-40.

Hadač, E. 1946. *The plant- communities of Sassen Quarter, Vestspitsbergen*, Studia Botanica Čechoslovaca.

Hansen, B. B., Isaksen, K., Benestad, R. E., Kohler, J., Pedersen, Å. Ø., Loe, L. E., Coulson, S. J., Larsen, J. O. & Varpe, Ø. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. *Environmental Research Letters,* 9.

Hansen, B. U., Sigsgaard, C., Rasmussen, L., Cappelen, J., Hinkler, J., Mernild, S. H., Petersen, D., Tamstorf, M. P., Rasch, M. & Hasholt, B. 2008. Present-Day Climate at Zackenberg. *Advances in Ecological Research.* Academic Press.

Harding, R. J., Gryning, S.-E., Halldin, S. & Lloyd, C. R. 2001. Progress in understanding of land surface/atmosphere exchanges at high latitudes. *Theoretical and Applied Climatology,* 70**,** 5-18.

Henry, G. H. R. & Molau, U. 1997. Tundra plants and climate change: the International Tundra Experiment (ITEX). *GLOBAL CHANGE BIOLOGY,* 3**,** 1-9.

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

Hovdal, S. B., Pelabon, C., Bremset Hansen, B. & Jónsdóttir, I. S. 2017. Effects of Experimental Winter Icing and Summer Warming on High Arctic Plant Phenology. NTNU.

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

Jónsdóttir, I. S. 2011. Diversity of plant life histories in the Arctic. *Preslia,* **83,** 281-300.

Kapfer, J. & Grytnes, J.-A. 2017. Large climate change, large effect? Vegetation changes over the past century in the European High Arctic. *Applied Vegetation Science,* 20**,** 204-214.

Katabuchi, M. 2015. LeafArea: an R package for rapid digital image analysis of leaf area. *Ecological Research,* 30**,** 1073-1077.

Korner- Nievergelt, F., Roth, T., Von Felten, S., Guelat, J., Almasi, B. & Korner- Nievergelt, P. 2015. Data Files and Functions Accompanying the Book: "Bayesian Data Analysis in Ecology using Linear Models with R, BUGS and Stan". Elsevier.

Körner, C. 1999. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. ,* Berlin, Springer- Verlag.

Lid, J. 1967. *Synedria of twenty vascular plants from Svalbard. ,* Botanische Jarhbücher.

Mallik, A. U., Wdowiak, J. V. & Cooper, E. J. 2011. Growth and Reproductive Responses of Cassiope tetragona, a Circumpolar Evergreen Shrub, to Experimentally Delayed Snowmelt. *Arctic, Antarctic and Alpine Research,* 43**,** 404-409.

Marr, K. L., Allen, G. A., Hebda, R., J. & Mccormick, L. J. 2013. Phylogeographical patterns in thewidespread arctic–alpine plant Bistorta vivipara (Polygonaceae) with emphasison western North America. *Journal of Biogeography,* 40**,** 847-856.

Mathez, E. A. 2009. *Climate Change : The Science of Global Warming and Our Energy Future,* New York, Columbia University Press.

Meziane, D. & Shipley, B. 1999. Interacting determinants of specific leaf area in 22 herbaceous species: effects of irradiance and nutrient availability. *Plant, Cell & Environment,* 22**,** 447-459.

Milner, J. M., Varpe, Ø., Van Der Wal, R. & Hansen, B. B. 2016. Experimental icing affects growth, mortality, and flowering in a high Arctic dwarf shrub. *Ecology and Evolution,* 6**,** 2139-2148.

Mundra, S., Bahram, M. & Eidesen, P. B. 2016. Alpine bistort (Bistorta vivipara) in edge habitat associates with fewer but distinct ectomycorrhizal fungal species: a comparative study of three contrasting soil environments in Svalbard. *Mycorrhiza,* 26**,** 809-818.

Phoenix, G. K. & Lee, J. A. 2004. Predicting impacts of Arctic climate change: Past lessons and future challenges. *Ecological Research,* 19**,** 65-74.

Preece, C. & Phoenix, G. K. 2014. Impact of early and late winter icing events on sub-arctic dwarf shrubs. *Plant Biology,* 16**,** 125-132.

Rønning, O. L. 1996. *The flora of Svalbard,* Oslo, NO, Norwegian Polar Institute.

Semenchuk, P. R., Gillespie, M. a. K., Rumpf, S. B., Baggesen, N., Elberling, B. & Cooper, E. J. 2016. High Arctic plant phenology is determined by snowmelt patterns but duration of phenological periods is fixed: an example of periodicity. *Environmental Research Letters,* 11.

Unander, S., Mortensen, A. & Elvebakk, A. 1985. Seasonal changes in crop content of the Svalbard Ptarmigan Lagopus mutus hyperboreus. *Polar Research,* 3**,** 239-245.

Van Der Wal, R. & Stien, A. 2014. High-arctic plants like it hot: a long-term investigation of between-year variability in plant biomass. *Ecology,* 95**,** 3414-3427.

Appendix

Table A1: Model selection table for abundance of *P. arctica, A. borealis* and *B. vivipara* with icing and warming as fixed effects forced to be in all models.

The global model for *P. arctica*: POAARC ~ icing x warming + NaturalIce + (1|Plot).

The global model for *A. borealis*: ALOBOR ~ icing x warming + NaturalIce + (1|Plot).

The global model for *B. vivipara*: BISVIV ~ icing x warming + NaturalIce + (1|Plot).

'+' indicate that the variable was included in the given model.

Species	Rank	Icing	warming	I:W	Natural ice	df	**AICc**	**ΔAICc**	***wi***
P. arctica	1	+	+		+	5	205.4	0.00	0.391
	2	+	+			4	205.6	0.16	0.362
	3	+	+	+	+	6	207.7	2.28	0.125
	4	+	+	+		5	207.8	2.33	0.122
A. borealis	1	+	+			4	306.0	0.00	0.536
	2	+	+	+		5	307.8	1.84	0.213
	3	+	+		+	5	308.1	2.14	0.184
	4	+	+	+	+	6	310.2	4.20	0.066
B. vivipara	1	+	+		+	5	145.3	0.00	0.533
	2	+	+			4	146.6	1.36	0.270
	3	+	+	+	+	6	148.1	2.87	0.127
	4	+	+	+		5	149.3	4.07	0.070

Table A2. Model selection table for flower production with icing and warming as fixed effect forced to be in all models.

The global model for *P. arctica*: Poa ~ icing x warming + NaturalIce + Abundance + (1|Block/Plot)

The global model for *A. borealis*: Alo ~ icing x warming + NaturalIce + Abundance + (1|Block/Plot),

The global model for *B. vivipara*: Bis ~ icing x warming + NaturalIce + Abundance+ (1|Block/Plot),

The global model for total flower production for the species: Flowers ~ icing x warming + NaturalIce + Abundance+ (1|Block/Plot) + (1|Species).

Abundance is number of hits from point frame analysis. '+' indicate that the variable was included in the given model.

Species	Rank	Icing	Warming	I:W	Natural ice	Abundance	df	AICc	ΔAICc	*wi*
P. arctica	1	+	+		+	+	7	314.5	0.00	0.296
	2	+	+			+	6	315.2	0.63	0.216
	3	+	+				5	316.2	1.62	0.132
	4	+	+	+	+	+	8	316.8	2.25	0.096
	5	+	+	+		+	7	317.1	2.54	0.083
A. borealis	1	+	+				5	156.2	0.00	0.445
	2	+	+			+	6	158.5	2.23	0.146
	3	+	+	+			6	158.6	2.31	0.140
	4	+	+		+		6	158.7	2.46	0.130
	5	+	+	+		+	7	160.8	4.55	0.046
B. vivipara	1	+	+				5	684.9	0.00	0.335
	2	+	+			+	6	686.3	1.38	0.168
	3	+	+	+			6	686.5	1.55	0.154
	4	+	+		+		6	686.9	2.02	0.122
	5	+	+			+	7	687.8	2.92	0.078
All species	1	+	+			+	7	2222.5	0.00	0.515
	2	+	+		+	+	8	2224.2	1.74	0.216
	3	+	+	+		+	8	2224.4	2.00	0.190
	4	+	+	+	+	+	9	2226.2	3.75	0.079
	5	+	+				6	2244.0	21.59	0.000

Table A3. Model selection table for inflorescence height with icing and warming as fixed effects forced to be in all models.
The global model for *P. arctica*: Height ~ icing x warming + NaturalIce + (1|Block/Plot)
The global model for *A. borealis*: Height ~ icing x warming + NaturalIce + (1|Block/Plot)
The global model for *B. vivipara*: Height ~ icing x warming + NaturalIce + (1|Block/Plot)
'+' indicate that the variable was included in the given model.

Species	Rank	Icing	warming	I:W	Natural ice	df	AICc	ΔAICc	*wi*
P. arctica	1	+	+			6	700.9	0.00	0.563
	2	+	+	+		7	702.9	1.96	0.211
	3	+	+		+	7	703.3	2.44	0.166
	4	+	+	+	+	8	705.4	4.47	0.060
A. borealis	1	+	+			6	393.4	0.00	0.653
	2	+	+	+		7	396.1	2.75	0.165
	3	+	+		+	7	396.3	2.95	0.149
	4	+	+	+	+	8	399.0	5.97	0.033
B. vivipara	1	+	+	+		7	1343.0	0.00	0.425
	2	+	+			6	1343.5	0.53	0.326
	3	+	+	+	+	8	1345.2	2.22	0.140
	4	+	+		+	7	1345.7	2.72	0.109

Table A4: Model selection table for *P. arctica* and *A. borealis* leaf length (throughout the season) with icing and warming as fixed effects forced to be in all models. The global model for *P. arctica*: Length ~ Round x icing x warming + NaturalIce + Observer + Withered + (1|Block/Plot/Leaf_number).
The global model for *A. borealis*: Length ~ Round x icing x warming + NaturalIce + Observer + Withered + (1|Block/Plot/Leaf_number).
Withered (0= still growing, 1= withered), where wither= more than half of the grass leaf was withered.
'+' indicate that the variable was included in the given model. R= Round, I= Icing, W= Warming.

Species	Rank	Round	Icing	Warming	N. ice	Observer	Withered	R:I	R:W	I:W	R:I:W	df	AICc	ΔAICc	*wi*
P. arctica	1	+	+	+	+		+					13	13910.0	0.00	0.458
	2	+	+	+	+	+	+					14	13911.9	1.94	0.174
	3	+	+	+	+		+			+		14	13912.0	2.03	0.166
	4	+	+	+	+	+	+			+		15	13914.0	3.97	0.063
	5	+	+	+	+		+	+				17	13914.2	4.20	0.056
A. borealis	1	+	+	+			+					12	26870.4	0.00	0.335
	2	+	+	+	+		+					13	26872.0	1.54	0.155
	3	+	+	+		+	+					13	26872.3	1.91	0.129
	4	+	+	+			+			+		13	26872.4	1.96	0.126
	5	+	+	+	+	+	+					14	26873.9	3.46	0.059

Table A5: Model selection table for *P. arctica* and *A. borealis* leaf length (peak season) with icing and warming as fixed effects forced to be in all models, and model selection table for *P. arctica* and *A. borealis* leaf length accounting for leaf weight (peak season) with icing and warming as fixed effects.
The global model for *P. arctica*: Length_fresh_mm ~ icing x warming + NaturalIce + (1|Block/Plot/Plant_number)
The global model for *A. borealis*: Length_fresh_mm ~icing x warming + NaturalIce + (1| Block/Plot/Plant_number),
The global model for *P. arctica*: Length_fresh_mm~ icing x warming + NaturalIce + Dry_weight_mg + (1|Block/Plot/Plant_number).
The global model for *A. borealis*: Length_fresh_mm~ icing x warming + NaturalIce + Weight_dried_mg + (1|Block/Plot/Plant_number).
'+' indicate that the variable was included in the given model.

Species	Rank	Icing	warming	I:W	Natural ice	Leaf weight	df	AICc	ΔAICc	*wi*
P. arctica	1	+	+				7	719.5	0.00	0.548
	2	+	+	+			8	721.3	1.80	0.223
	3	+	+		+		8	722.0	2.42	0.164
	4	+	+	+	+		9	723.8	4.27	0.065
A. borealis	1	+	+				7	805.2	0.00	0.583
	2	+	+	+			8	807.5	2.26	0.189
	3	+	+		+		8	807.6	2.42	0.174
	4	+	+	+	+		9	809.9	4.74	0.054
P. arctica	1	+	+			+	8	673.4	0.00	0.556
	2	+	+	+		+	9	675.2	1.85	0.221
	3	+	+		+	+	9	675.8	2.48	0.161
	4	+	+	+	+	+	10	677.7	4.39	0.062
	5	+	+				7	719.5	46.19	0.000
A. borealis	1	+	+			+	8	694.4	0.00	0.435
	2	+	+	+		+	9	694.9	0.48	0.321
	3	+	+		+	+	9	696.9	2.45	0.128
	4	+	+	+	+	+	10	697.5	3.03	0.096
	5	+	+				7	805.2	110.77	0.000

Table A6. Model selection table for *B. vivipara* leaf length (peak season) with icing and warming as fixed effects forced to be in all models, and model selection table for *B. vivipara* leaf length accounting for leaf width (peak season) with icing and warming as fixed effects.

The global model for leaf length: leaf_length_mm ~ icing x warming x DevelopmentStage + NaturalIce + (1|Block/Plot/Square).

The global model for leaf length accounting for leaf weight: leaf_length_mm ~ icing x warming x DevelopmentStage + NaturalIce + leaf_width_mm + (1|Block/Plot/Square). DevelopmentStage = indicating if the given leaf was from *B. vivipara* reproductive or *B. vivipara* vegetative.

'+' indicate that the variable was included in the given model.

Species	Rank	Icing	Warming	DevelopmentStage	Natural ice	width	DS:I	DS:W	I:W	DS:I:W	df	AICc	ΔAICc	W_i
B. vivipara	1	+	+	+							8	1972.1	0.00	0.156
	2	+	+	+				+			9	1972.4	0.31	0.133
	3	+	+	+			+	+	+	+	12	1972.9	0.80	0.105
	4	+	+	+					+		9	1973.8	1.71	0.066
	5	+	+	+				+	+		9	1974.1	2.05	0.057
B. vivipara	1	+	+			+					8	1938.5	0.00	0.284
	2	+	+	+		+					9	1940.3	1.81	0.115
	3	+	+			+			+		9	1940.5	2.02	0.104
	4	+	+		+	+					9	1940.5	2.03	0.103
	5	+	+	+		+		+			10	1941.4	2.89	0.067

Table A7: Model selection table for *P. arctica*, *A. borealis* and *B. vivipara* leaf weight (peak season) with icing and warming as fixed effects forced to be in all models. The global model for *P. arctica*: Dry_weight_mg ~ icing x warming + NaturalIce + (1|Block/Plot/Plant_number). The global model for *A. borealis*: Dry_weight_ dreied_mg ~ icing x warming + NaturalIce + (1|Block/Plot/Plant_number). The global model for *B. vivipara*: Dry_weight_mg ~ icing x warming + NaturalIce + (1|Block/Plot). '+' indicate that the variable was included in the given model.

Species	Rank	Icing	warming	I:W	Natural ice	df	AICc	ΔAICc	*wi*
P. arctica	1	+	+			7	366.5	0.00	0.517
	2	+	+	+		8	368.0	1.56	0.237
	3	+	+		+	8	368.7	2.23	0.170
	4	+	+	+	+	9	370.3	3.82	0.077
A. borealis	1	+	+			7	497.6	0.00	0.571
	2	+	+	+		8	499.8	2.13	0.197
	3	+	+		+	8	500.0	2.38	0.174
	4	+	+	+	+	9	502.2	4.54	0.059
B. vivipara	1	+	+			6	701.3	0.00	0.556
	2	+	+		+	7	703.4	2.11	0.193
	3	+	+	+		7	703.5	2.18	0.187
	4	+	+	+	+	8	705.6	4.33	0.064

Table A8: Model selection table for *P. arctica* and *A. borealis* leaf weight accounting for leaf length (peak season) with icing and warming as fixed effects forced to be in all models.
The global model for *P. arctica*: Dry_weight_mg ~ icing x warming + NaturalIce + Length_fresh_mm (1|Block/Plot/Plant_number). The global model for *A. borealis*: Dry_weight_mg ~ icing x warming + NaturalIce + Length_fresh_mm (1|Block/Plot/Plant_number).
'+' indicate that the variable was included in the given model.

Species	Rank	Icing	Warming	I:W	Natural ice	Leaf length	df	AICc	ΔAICc	*wi*
P. arctica	1	+	+			+	8	322.6	0.00	0.559
	2	+	+		+	+	9	324.5	1.98	0.208
	3	+	+	+		+	9	324.9	2.38	0.170
	4	+	+	+	+	+	10	327.0	4.39	0.062
	5	+	+				7	366.5	43.91	0.000
A. borealis	1	+	+			+	8	385.0	0.00	0.428
	2	+	+	+		+	9	385.4	0.42	0.346
	3	+	+		+	+	9	387.4	2.42	0.128
	4	+	+	+	+	+	10	387.9	2.96	0.097
	5	+	+				7	497.6	112.65	0.000

Table A9: Model selection table for *B. vivipara* leaf width (peak season) with icing and warming as fixed effects forced to be in all models, and dredge model selection table for *B. vivipara* leaf width accounting for leaf length (peak season) with icing and warming as fixed effects.
The global model for leaf width: leaf_width_mm ~ icing x warming x DevelopmentStage + NaturalIce + (1|Block/Plot/Square).
The global model for leaf width accounting for leaf length: leaf_width_mm ~ icing x warming x DevelopmentStage + NaturalIce + leaf_length_mm + (1|Block/Plot/Square). DevelopmentStage (DS) = indicating if the given leaf was from *B. vivipara* reproductive or *B. vivipara* vegetative.
'+' indicate that the variable was included in the given model.

Species	Rank	Icing	Warming	DevelopmentStage	Natural ice	length	DS:I	DS:W	I:W	DS:I:W	df	AICc	ΔAICc	W_i
B. vivipara	1	+	+	+			+	+	+	+	12	1373.3	0.00	0.397
	2	+	+	+	+		+	+	+	+	13	1375.5	2.17	0.134
	3	+	+	+					+		9	1376.8	3.51	0.069
	4	+	+	+							8	1376.9	3.55	0.067
	5	+	+	+					+		10	1377.8	4.48	0.042
B. vivipara	1	+	+	+		+					9	1341.2	0.00	0.161
	2	+	+	+		+			+		10	1341.8	0.60	0.119
	3	+	+	+		+	+	+	+	+	13	1342.1	0.90	0.103
	4	+	+	+		+	+				10	1342.2	1.03	0.096
	5	+	+	+		+	+		+		11	1342.7	1.54	0.074

Table A10: Model selection table for *B. vivipara* specific leaf area (SLA) and surface area with icing and warming as fixed effects forced to be in all models. The global model for SLA: SLA ~ icing x warming + NaturalIce + (1|Block/Plot). The global model: surface area ~ icing x warming + NaturalIce + (1|Block/Plot). '+' indicate that the variable was included in the given model.

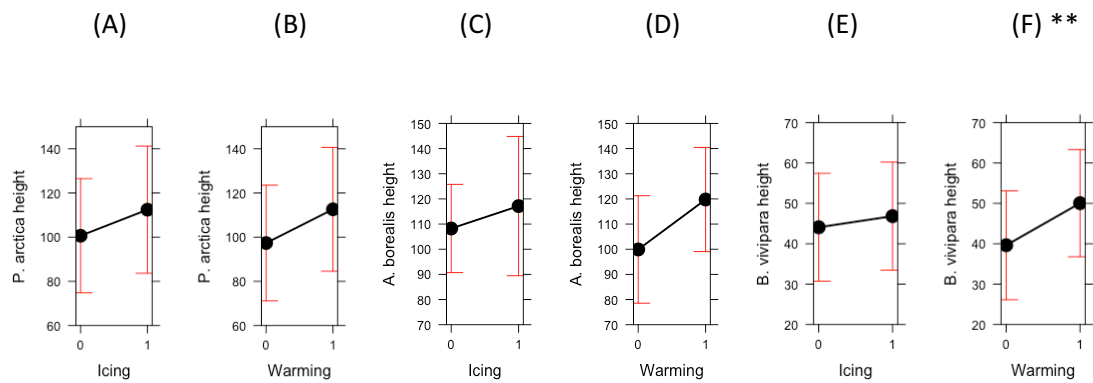| Species	Variable	Rank	Icing	warming	I:W	Natural ice	df	AICc	ΔAICc	*wi*
B. vivipara	SLA	1	+	+	+		7	2871.3	0.00	0.333
		2	+	+			6	2871.4	0.15	0.308
		3	+	+	+	+	8	2872.3	1.03	0.199
		4	+	+		+	7	2872.7	1.46	0.160
B. vivipara	Surface area	1	+	+			6	1491.3	0.00	0.492
		2	+	+	+		7	1492.7	1.41	0.243
		3	+	+		+	7	1493.3	2.02	0.179
		4	+	+	+	+	8	1494.8	3.50	0.085

Figure A1. Effect plot of icing (A, C, E) and warming (B, D, F) on *P. arctica* (A, B), *A. borealis* (C, D) and *B. vivipara* (E, F) inflorescence height. ** indicate that p < 0.01.
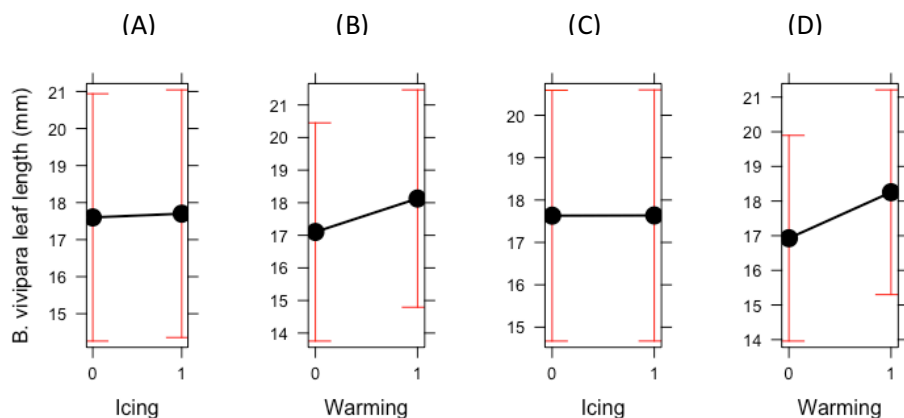

Figure A2. Effect plot of *B. vivipara* leaf length (mm) of icing (A), warming (B), and *B. vivipara* leaf length accounting for leaf width of icing (C) and of summer warming (D).