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Effects of Experimental Winter Icing and Summer Warming on High Arctic Plant Phenology

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Master of Science
Submission date: December 2016
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Abstract

Climate change is expected to have pronounced effects in the Arctic, causing increased temperatures and changes in winter precipitation patterns. For instance, extreme winter rain events often result in ground ice formations covering the vegetation. These alterations in temperature and precipitation are expected to cause phenological changes in high Arctic plant species by, for instance, altering plant growing conditions or the length of the growing season. We examined phenological responses (reproductive and vegetative) to climate change, in a full factorial field experiment in high Arctic Svalbard (78°N). Here, we simulated an extreme mid-winter rain on snow event by experimentally adding water and encapsulating the vegetation in solid ice during winter 2015/2016, and increased summer temperatures by open top chambers. During summer 2016, we investigated the effect of treatments (warming, icing and the combination of warming and icing) on the phenology of key vascular species, *Salix polaris, Bistorta vivipara, Poa arctica, Alopecurus borealis* and *Luzula confusa*. The icing treatment caused on average three days delay in spring melt and had a general tendency to delay reproductive phenology with the approximately same magnitude, yet we have large variation between species and phenophases. This overall delay tended to diminish through the season. In contrast, the warming treatment advanced reproductive phenology with about 2 – 8 days, across all species over the summer, with pronounced effect on phenophases involving floral development and seed maturation. The combined icing and warming treatment advanced phenology to a lesser extent than the warming treatment alone, indicating that warmer temperatures mitigate the effect of delayed spring onset due to later melting time. We found no treatment effect on vegetative phenology. Phenological changes can have consequences for plant fitness and may affect key ecosystem components, in addition to trophic interactions. By documenting phenological alterations in key Arctic tundra species as a consequence of warmer temperatures and ice encapsulation, this study gives insight into how high Arctic tundra vegetation could respond to the predicted future climate change. Further investigations on possible delayed phenological effects and other plant traits, such as seed germinability, are needed in order to further understand the effect of climate change on fitness.

Abstract in Norwegian

Klimaendringer er forventet å ha sterk effekt i Arktis med økt temperatur og endrede nedbørsmønstre om vinteren. For eksempel vil episoder med ekstremt vinterregn ofte resultere i dannelsen av bakkeis som dekker vegetasjonen. Disse endringene i temperatur og nedbør er forventet å forårsake endringer i fenologien hos Arktiske plantearter, ved for eksempel å endre lengden på vekstsesongen. Vi undersøkte fenologiske responser (vegetative og reproduktive) på klimaendringer i et fullt faktorielt felteksperiment i høyarktiske Svalbard (78°N). Her simulerte vi ekstremt vinterregn ved å eksperimentelt påføre vann og innkapsle vegetasjonen i solid is under vinteren 2015/2016 og økte sommertemperaturen med ”open top chambers” (drivhus uten tak). Gjennom sommeren 2016 studerte vi effekten av behandlingene (varme, is og kombinasjonen av is og varme) på fenologien av de vaskulære nøkkelartene *Salix polaris, Bistorta vivipara, Poa arctica, Alopecurus borealis* and *Luzula confusa.* Is-behandlingen førte til en forsinkelse i vårsmeltingen på i gjennomsnitt tre dager og hadde en generell tendens til å forsinke reproduktiv fenologi i omtrent samme grad, men det er stor variasjon mellom arter og fenofaser. Denne generelle forsinkelsen viste en tendens til å avta gjennom sesongen. Varmebehandlingen framskyndet reproduktiv fenologi på tvers av alle arter over sommeren, med en generelt sterkere effekt på fenofaser som omfatter blomsterutvikling og frømodning. Den kombinerte is- og varmebehandlingen framskyndet fenologien i mindre grad enn varmebehandlingen alene, noe som indikerer at økte temperaturer kan redusere effekten av forsinket vårstart som følge av senere issmelting. Vi fant ingen effekt av behandlingene på vegetativ fenologi. Fenologiske endringer kan ha konsekvenser for reproduktiv suksess hos planter og kan påvirke viktige økosystemkomponenter, i tillegg til trofiske interaksjoner. Ved å dokumentere fenologiske endringer hos arktiske nøkkelarter som en konsekvens av varmere temperaturer og isdannelse, gir denne studien innsikt i hvordan høyarktisk vegetasjon kan respondere på fremtidige klimaendringer. Videre undersøkelser av mulige forsinkede fenologiske effekter samt andre plantetrekk som frøspiring trengs for bedre innsikt i effekten av klimaendringer på fitness.

Contents

Introduction

Climate change has a widespread impact on a broad range of life forms and ecosystems around the world (Walther et al. 2002, Parmesan and Yohe 2003, Parmesan 2006, IPCC 2014). A pronounced effect of the changing climate is extensive shifts in phenology (i.e. the timing of plants and animals' seasonal activities) across taxa and within a variety of geographical areas (Parmesan 2006, Denny et al. 2014). These phenological alterations come as a consequence of shifts in the timing of seasons, such as earlier spring onset (Høye et al. 2007). Regarding plants, phenology influences the ability to utilize resources for reproduction and growth. For instance, the timing of the reproductive phenophases in plants will be critical to obtain optimal seed set and hence optimal timing of seed dispersal (Cleland et al. 2007). Thus, if reproductive processes fail to coincide with the time window of favourable conditions, this can have large consequences for fitness (Visser and Both 2005). Because phenology is a highly responsive plant trait to climate change (Molau and Edlund 1996, Cleland et al. 2007), observations of phenological development in plants, could contribute to increased understanding of how the vegetation responds to global warming. Changes in phenological patterns may have consequences for ecosystem functioning and processes (Denny et al. 2014) and could influence interactions between ecosystem components (Iversen et al. 2009), such as herbivores, seed dispersers and pollinators (Brody 1997). To study phenology is hence important for understanding future ecosystem changes (Oberbauer et al. 2013).

In the Arctic, climate change is expected to have particularly strong effects, as the average increase in temperature is exceeding the global mean, at almost twice the rate (Overpeck et al. 1997, IPCC 2014). In addition, this is expected to cause an increased frequency of extreme weather events in the Arctic, which already have harsh and unpredictable weather conditions (Walsh et al. 2005, Weatherhead et al. 2010). This could for instance be in form of heavy rain and more frequent warm periods during winter (Rennert et al. 2009, IPCC 2014). It has been shown that rain on snow (ROS) events in mid-winter tend to result in the formation of solid ground ice in some Arctic areas. The rain melts the snow and freezes to solid ice on the deeply frozen ground (Putkonen and Roe 2003, Kohler and Aanes 2004, Rennert et al. 2009, Hansen et al. 2014). This ground-ice layer could build up to a thickness of 20 cm and cover most of the short-growing Arctic vegetation (Hansen et al. 2014). While the effects of such ground icing *per se* remain to be explored, it is well documented that changes in snow conditions during winter, and particularly snow depth, can influence plant phenology by changing the timing of

melting processes (Cooper 2014). For high Arctic plants, both time of melting in spring and temperature during the short growing season is crucial for plant development (Chapin III 1983, Høye et al. 2007, Cooper et al. 2011). Consequently, stronger phenological shifts can be expected in Arctic areas than elsewhere.

The growing season in the High Arctic starts shortly after snowmelt (e.g. in early June in the lowlands of central Svalbard) (Malnes et al. 2010) and some plants are already starting to senescence in early August, making the season very short (Cooper et al. 2011). However, earlier spring onset due to warmer temperatures (or less snow) and earlier melting might give a longer growing season and advance plant phenology development (Høye et al. 2007, Cooper 2014). Accordingly, studies on the effect of experimentally increased temperatures have shown advanced phenology and increased reproductive success in some species. Results from a meta-analysis on responses of tundra plants on experimental warming done by Arft et al. (1999) revealed that key phenophases, such as bud burst and flowering happened earlier in warmed plots. Wookey et al. (1993) found that enhanced temperatures had striking effects in advancing phenology and improving seed-setting of some high Arctic plant species.

Despite warmer temperatures, some climate scenarios predict more snowfall in parts of the Arctic due to increased precipitation in winter (Saha et al. 2006). This could potentially lead to later melting, which is expected to delay plant phenology and give an even shorter growing season (Cooper et al. 2011). Some plant species might therefore not be able to set seed before the end of season, causing reduced reproductive success and poor prognosis for long-term survival (Cooper et al. 2011). As with increased snowfall, a thick ice-cover could also be expected to cause different melting time (i.e. when the ground is barren) compared with ice-free ground. Empirical field studies are still lacking, and the consequences for phenology and fitness of extreme icing events for Arctic tundra plants are not well documented. Nevertheless, a recent study by Milner et al. (2016) found that icing had severe effects on shoot survival and flowering in the evergreen dwarf shrub *Cassiope tetragona.* In addition, a few experimental studies from the sub-Arctic suggest that icing may have contrasting effects on phenology and reproduction across taxa and functional groups. For instance, Preece et al. (2012) simulated ice encasement of three dwarf shrub species in northern Sweden over a three-year period. They found delayed leaf emergence and reduced budburst in the evergreen dwarf shrub *Vaccinium vitis-idaea* the first year, but no effect in the following years, and concluded that these species are relatively tolerant to icing. Bokhorst et al. (2008) simulated an extreme winter warming

event, followed by extreme cold in sub-Arctic dwarf shrub heathland in northern Sweden. The results demonstrated that such winter events caused delayed bud development, reduced bud production and impaired reproductive effort in some species. However, the extent to which these studies can be generalized to ice encasement of high Arctic tundra vegetation is highly questionable. To our knowledge, no studies have so far investigated the impact of icing on the timing of spring onset (i.e. ice melting) and spring-summer phenology in Arctic tundra plants.

In addition to a potential delay in melting processes, ice encasement of vegetation can expose plants to oxygen depletion due to the ice being less permeable to gas transfer than snow (Gudleifsson 1997, Albert and Perron 2000). This could result in cell death due to the ceasing aerobic respiration (Pfister-Sieber and Braendle 1994). Ice encasement will also expose plants to lower temperatures compared to snow, which has a stronger insulating effect (Pomeroy and Brun 2001, Callaghan et al. 2004). This could lead to cellular dehydration and cell damage (Preece and Phoenix 2014). However, Arctic plant species may have a better tolerance of anoxia than similar species at lower latitudes (Crawford et al. 1994).

In this study, we investigated how the phenology of five key tundra vascular plant species in high Arctic Svalbard is affected by climate change in form of ground-ice-formation due to warm spells in winter and summer-warming. To achieve this, both an extreme mid-winter rain-on-snow event and a warmer summer were simulated in moss tundra vegetation following a full factorial design. Ice encasement was applied to simulate the environmental changes due to ROS events, and open top chambers (OTC's) were used to induce summer warming. OTC's are widely used in experimental studies of climate warming effects in plants, both in the Arctic and in alpine regions (Henry and Molau 1997, Bokhorst et al. 2013). During spring and summer 2016, phenology of five abundant species, representing different growth forms and important food sources for herbivores in Svalbard, were monitored.

We hypothesized I), that warmer air temperatures (induced by OTCs) after snow melt advances the plant phenological development due to improved growing conditions. We predicted that the reproductive and vegetative phenology of our key plant species occurs more rapidly (Wookey et al. 1993, Arft et al. 1999) and, hence, is reaching specific phenophases earlier compared to controls. II), based on previous observations of natural icing events (B. B. Hansen, pers. comm.), we hypothesized that the icing treatment causes a delay in the timing of spring melting processes, (i.e. later snow/ice-free ground) and hence delays phenology. We predicted the same

magnitude of initial time delay in the plants' phenological development, thereby reaching specific phenophases later (compared to controls). An even more delayed phenology than the actual time delay in ice melt would indicate an additional effect of the ice treatment *per se* (e.g. damage due to anoxia as indicated by Preece and Phoenix (2014)). Yet we had no *a priori* expectations of such effects. III), for the combined icing and warming treatment, we expected an initial delay in phenology (due to the icing effect) and a faster catch-up effect during the season than with icing only (due to the warming effect).

Methods

Study area and key species

The study area was situated in Adventdalen valley in Spitsbergen, Svalbard (78° 13`N, 15° 38`E) (Figure 1). The valley is close to the settlement of Longyearbyen, located in the central area of the island Spitsbergen. The climate is cold with harsh weather conditions and fairly low precipitation. However, there has been a tendency towards warmer and rainier winters in later years (Figures 2 and 3). Figure 2 presents the annual mean temperature in spring (May) (mean = -3.4 °C, SD = 1.9 °C) and summer (June – August) (mean = 4.7 °C, SD = 1.0 °C) for the period 1960 – 2016 and in winter (November – April) (mean = -11.9 °C, SD = 2.8 °C) for 1960 - 2015. Figure 3 presents annual winter (November – April) precipitation, separated in snow (mean = 88.5 mm, SD = 24.9 mm) and rain (mean = 12.6 mm, SD = 16.6 mm), for the period 1960 – 2015 (mean total winter precipitation was 101.0 mm, SD = 29.4 mm). Adventdalen lies in the bioclimatic sub-zone C, characterized by wet to dry tundra (Walker et al. 2005). The study sites were located in mesic habitats in levelled or gently sloping terrain, with moss tundra vegetation (Rønning 1996, Vanderpuye et al. 2002), dominated by the mosses *Sanionia uncinata, Tomentypnum nitens and Polytrichum spp.*, the deciduous dwarf shrub *Salix polaris,* the herb *Bistorta vivipara* and the graminoids *Alopecurus borealis, Poa arctica* and *Luzula confusa.* The area is heavily grazed by reindeer (*Rangifer tarandus platyrhynchus*) year round, and barnacle geese (*Branta leucopsis*) and pink footed geese (*Anser brachyrhynchus*) in spring and late summer.

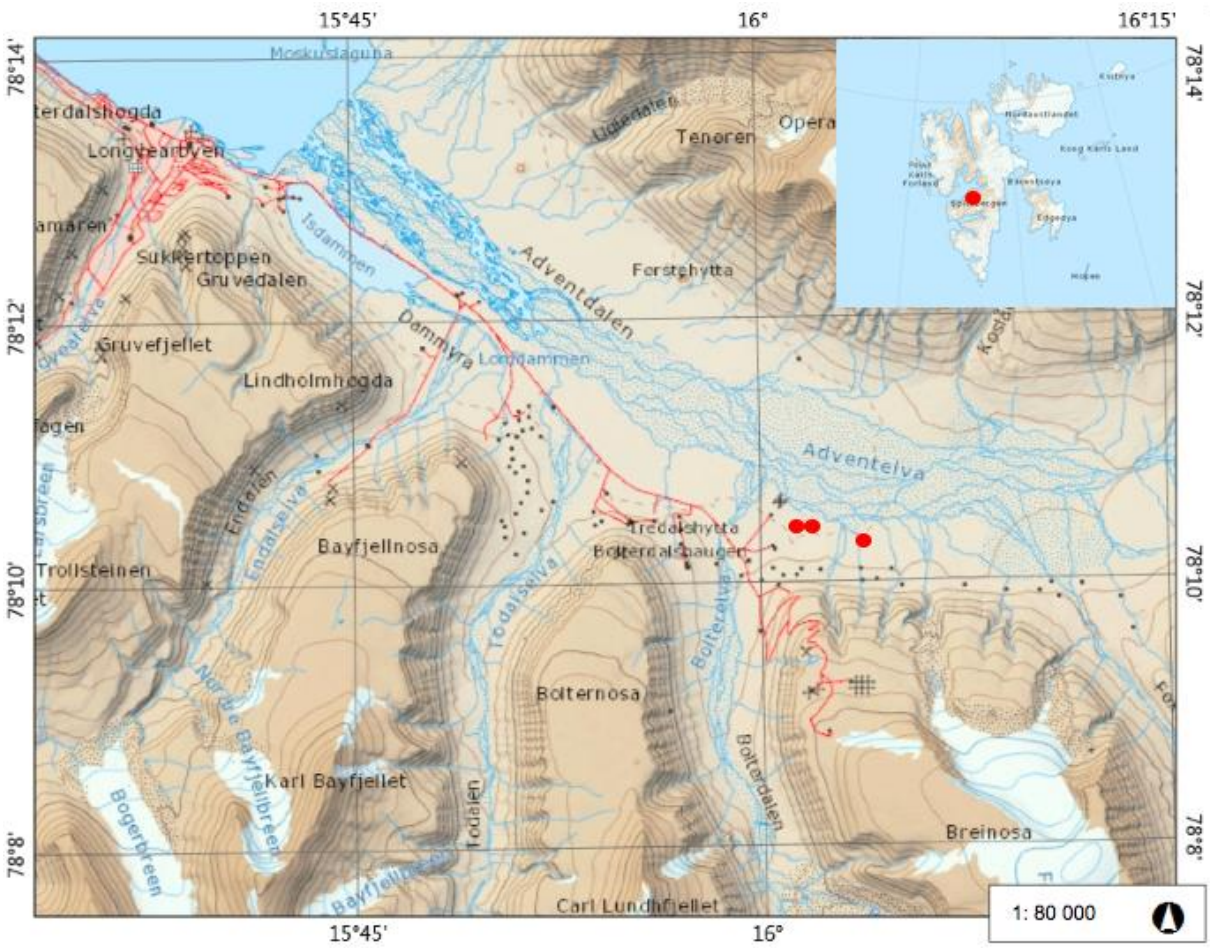


Figure 1: The location of the three study sites in Adventdalen valley, Svalbard, marked with red points. Longitude– latitude coordinates is shown at the map border and map scale in the bottom-right corner. The map is made in ArcGIS Rest API 10.11. © Norwegian Polar Institute.

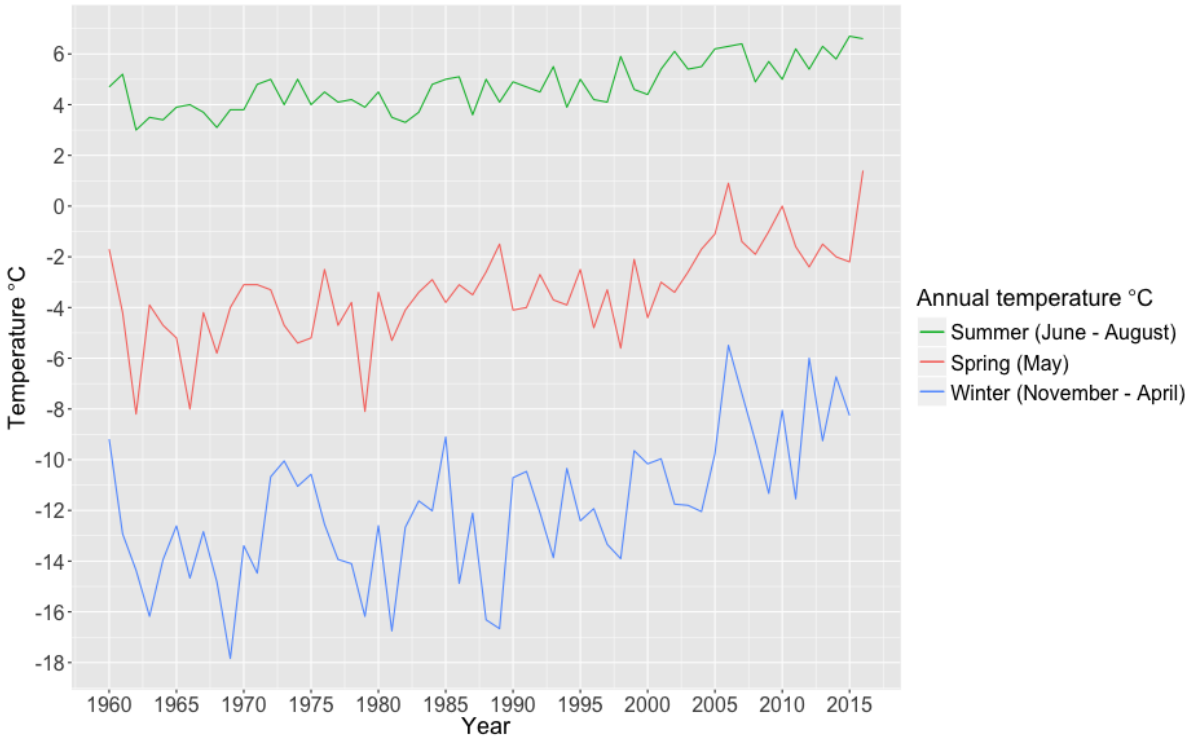


Figure 2. Annual mean spring (May) and summer (June – August) temperature for the period 1960 – 2016 and mean winter (November – April) temperature for 1960 – 2015 (www.eklima.no).

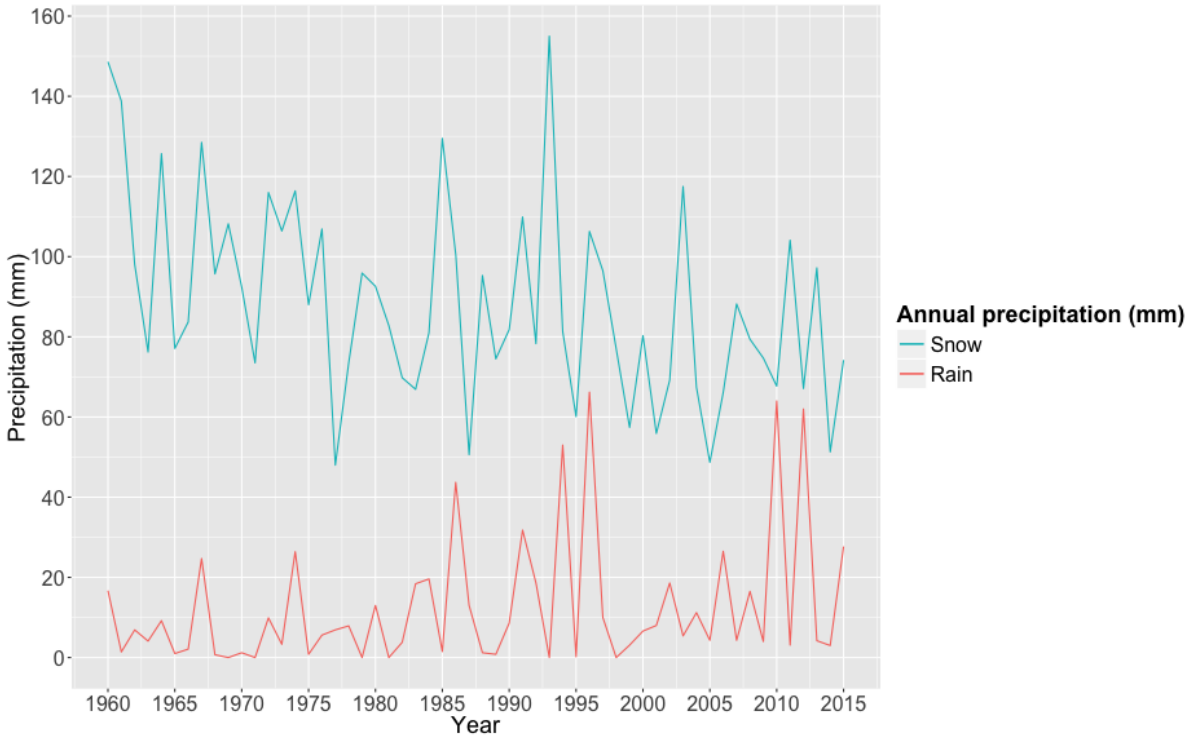


Figure 3. Annual mean winter (November – April) precipitation (mm) separated in snow and rain for the period 1960 – 2015 (www.eklima.no).

In this experiment we studied five common and widespread species (Rønning 1996); *Salix polaris* Wahlenb, *Bistorta vivipara* (L.) Gray, *Poa arctica* R.Br, *Alopecurus borealis* Trin. *and Luzula confusa* Lindeb.

Salix polaris is a perennial, dioecious dwarf shrub with a creeping stem and rhizomes. The vertical part of the stem extending out of the moss carpet is short (<5 mm) with small, oval, dark green leaves (about 1 cm diameter), which shifts early to autumn color. It reproduces sexually and vegetatively by rhizomes (Rønning 1996, Dormann and Skarpe 2002, Muraoka et al. 2002). *Bistorta vivipara* is a perennial, rhizomatous herb (3 - 10 cm) with almost exclusively asexual reproduction provided by bulbils produced at the lower part of the inflorescences. Sexual reproduction is rare (Callaghan 1973, Soyrinki 1989, Bauert 1993). Its thick rhizome functions as important nutrient storage organ, which enables earlier start of growth in spring (Monson et al. 2006). *Poa arctica* is a perennial grass species with 10 - 15 cm tall inflorescences. It has asexual reproduction by long rhizomes and plantlets if viviparous (pseudovivipary) (Rønning 1996, Bakker and Loonen 1998). *Alopecurus borealis* is a perennial grass with 15 - 25 cm tall inflorescences (Rønning 1996). It has sexual reproduction (although there is generally low seed germination) and efficient local vegetative reproduction by long rhizomes (Müller et al. 2011). *Luzula confusa* is a perennial, caespitose rush species with 10 - 15 cm tall inflorescences (Rønning 1996), and reproduces vegetatively by tillering (Addison and Bliss 1984).

All species are important forage species for both resident and migratory herbivores. *L. confusa* and *S. polaris* are key food plants of the resident Svalbard reindeer (*Rangifer tarandus platyrhynchus*) diet in winter and early spring (Bjørkvoll et al. 2009) and early in the growing season (Van der Wal et al. 2000). *A. borealis, B. vivipara, and P. arctica are* important components of the barnacle goose (*Branta leucopsis*) diet (Bakker and Loonen 1998, Sjögersten et al. 2010). In addition, *B. vivipara* is the only food item of ptarmigan chicks (Unander and Steen 1985) and its rhizomes are an important food source for pink-footed geese (*Anser brachyrhynchus*) during pre-breeding (Fox and Bergersen 2005, Fox et al. 2006).

Experimental design

The effects of experimental winter icing and summer warming on plant phenology has been assessed using a full factorial generalized randomized block design. This includes three replicated experimental units for each treatment within each of three blocks (Figure 4). In Adventdalen, three sites (approximately 20 x 20 m) with relatively homogeneous mesic moss tundra vegetation were selected at the end of summer 2015 by collaborators at UNIS. The three sites were in a distance between 150 m and 780 m from each other, with other vegetation types in between. Each site will be referred to as a block in the experiment. In each block, twelve homogenous 80 cm x 80 cm plots were selected and marked at least 2 m apart from each other. In each block, following a randomization process, three plots were assigned each of the treatment combinations.

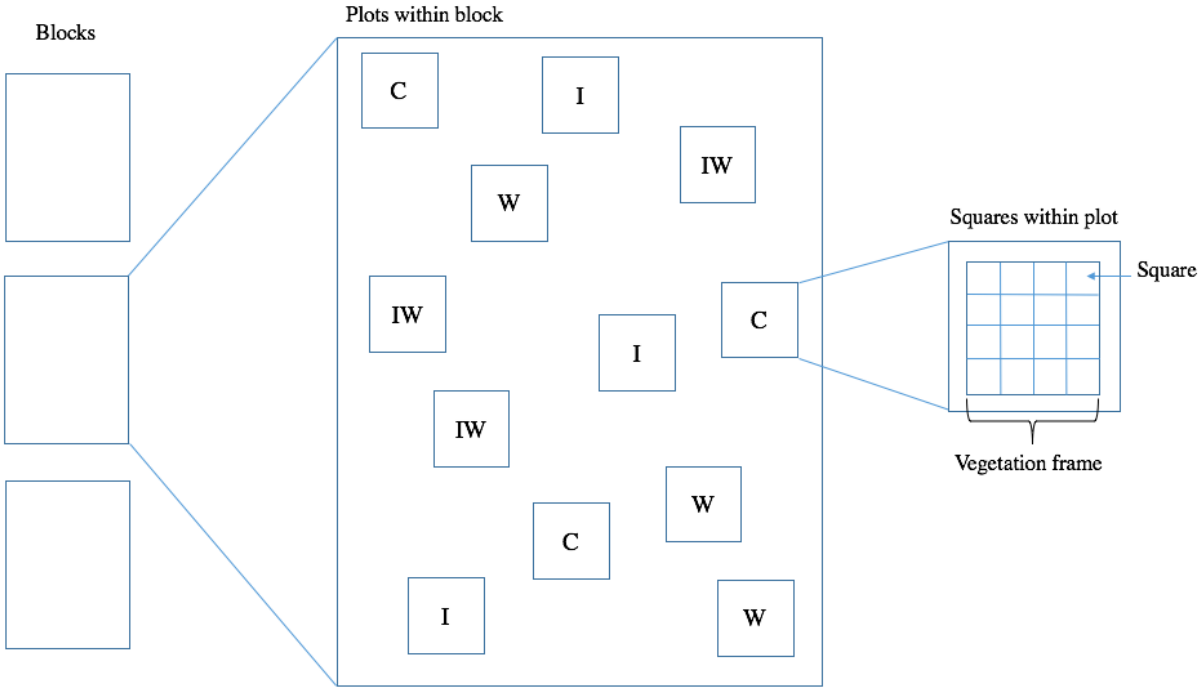


Figure 4: Illustration of experimental design. In total, 36 plots were established (12 plots in each of the three blocks) with nine plots per treatment in total (three plots of each treatment per block). C = control plots, I = plots treated with icing, IW = plots treated with icing and warming and W = plots treated with warming. Each plot was subdivided in 16 sub-squares by a vegetation frame during phenology registrations.

Experimental treatments consisted of two levels of warming (ambient temperatures and experimental warming) and two levels of icing (no icing and experimental icing), resulting in four treatment combinations. The control units (C) received no treatment. The icing-no warming treatment (I) involved covering the vegetation within the plot area in solid ice (see details below), which simulated the icing effect that occurs after ROS on Svalbard (Figure 5 a). Plots that received the warming – no icing (W) treatment had open top chambers (OTC's) through the season, placed out after snow melt, to increase temperatures (Figure 5 d). The treatment combining icing and warming (IW) involved placing an OTC on plots that also received the icing treatment. All plots were covered by metal nets for grazing protection from 29th of May, to avoid herbivory as a confounding factor, as herbivores may modify the composition of plants through feeding selection (Van der Wal et al. 2000). In addition, herbivory is expected to differ between ambient and warmed plots, since OTCs may act as a barrier against herbivores.

In January 2016, the 18 plots selected for icing treatment (I and IW) were re-located for preparation. Snow depth (mean = 5.1 cm, SD = 1.9 cm) and the natural occurrence of ice (if present) (mean = 0.9 cm, SD = 1.2 cm) was measured in each plot. The snow was removed from the plot area, to get the ice as dense as possible. In each of these plots, a 13 cm high 60 cm x 60 cm wooden frame was placed on the ground. The icing treatment itself was performed on 4th – 5th February 2016 under cold weather conditions. The wooden frame was gradually filled with cold water from 20 litre cans (mixed with snow) which were brought to the experimental site by snow mobiles. The ice encasement occurred gradually over two days until the wooden frames were filled with solid ground-ice (mean = 13,1 cm, SD = 1.1 cm), mimicking the natural ground-ice building up after heavy ROS events (see Milner et al. 2016 for details).

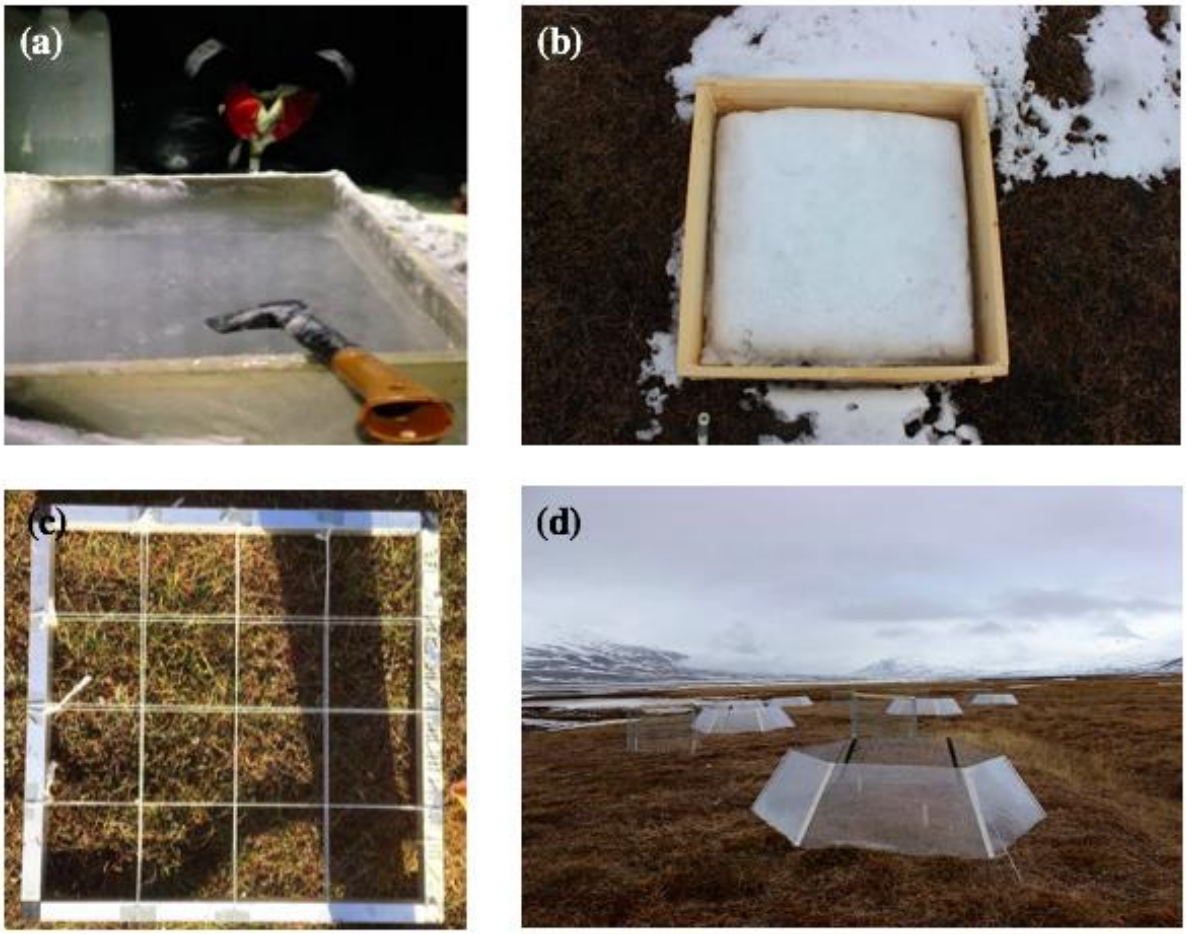


Figure 5: (a) A wooden frame filled with ice-water. (b) Icing plot during spring melt (photo taken on 15th May). Snow covers the remaining ice. (c) Vegetation frame used for phenology monitoring. (d) Open top chambers covering plots at the study site.

During winter 2015/2016 (November - April), soil surface temperature was measured in two icing plots (mean = -7.6 °C, SD = 3.9 °C) and two control plots (mean = -7.7 °C, SD = 3.8 °C) in each block. The wooden frames were removed at melting to avoid confounding microclimatic effects. Time of snowmelt and melting of ice (in the icing treatment) was estimated as the first day in May when temperature loggers (at soil surface) in control plots and iced plots respectively, registered temperatures exceeding 0 °C, applying a linear mixed model with block as random intercept effect (day of snowmelt in May: mean ± SE = 11.17 ± 3.00, day of ice melting in May: mean ± SE = 14.00 ± 3.13). Thus, the ground was barren approximately between 11th – 17th May. Figure 5 b illustrates the delay in ice melt compared to snow melt. On May 23rd, after all snow and ice had melted, OTCs were placed on plots receiving the W and IW treatment. Soil surface temperature was measured during the summer in each plot (Figure

6) (warmed plots: mean = 7.3 °C, SD = 1.4 °C, control plots: mean = 6.3 °C, SD = 1.5 °C). Summer air temperatures at 10 cm above the surface were measured by HOBO-loggers inside one OTC (mean temperature = 9.4 °C, SD = 2.9 °C) and at one control plot (mean temperature = 8.5 °C, SD = 2.3 °C).

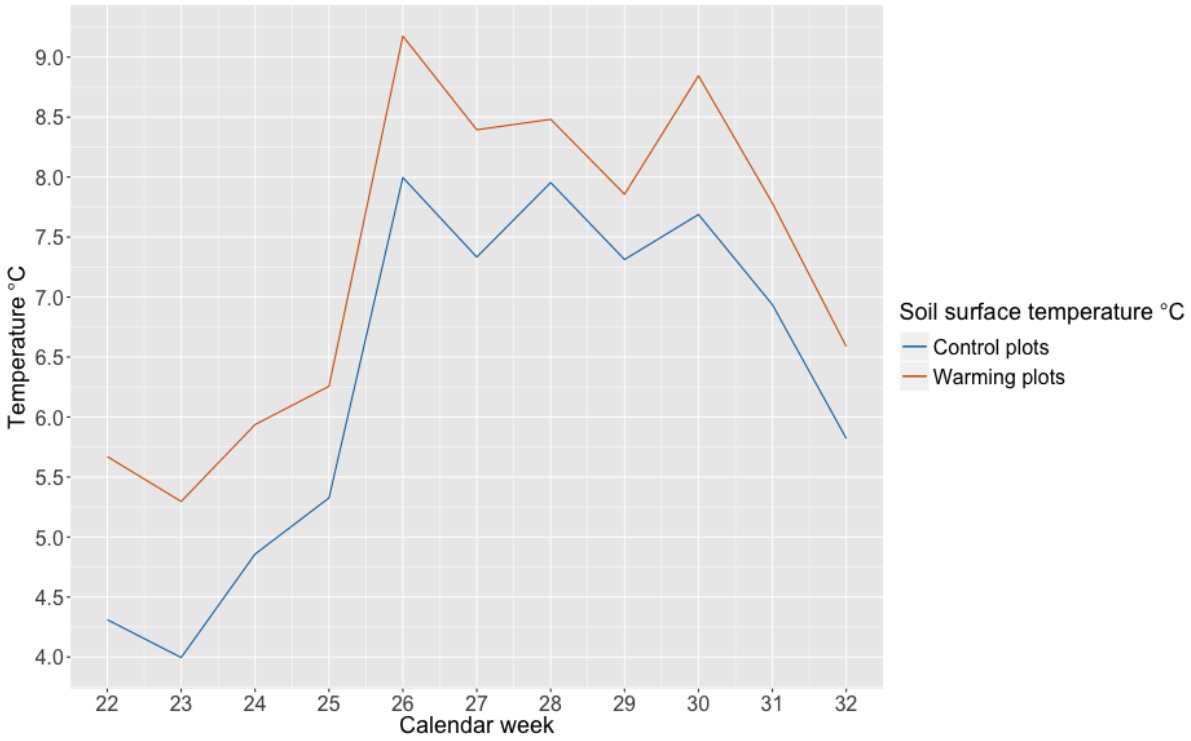


Figure 6. Mean weekly soil surface temperature in control plots and warmed plots in summer 2016.

In summer 2016, we recorded phenology during repeated rounds of observations which lasted for 1-2 days, with 2 - 6 days in between each round (4.5 days in average). We increased the number of days between each round as the phenological development slowed down during the season. The first round of observation was done on the 22th and 23rd of June and the last round was done 11th and 12th of August. The observations went thus over 51 days in total, (i.e. 12 rounds of observations). While monitoring the phenology, a 50 cm x 50 cm frame (leaving a 5 cm edge of the 60 x 60 cm area made by the wooden frame, to minimize edge effects), subdivided in 16 sub-squares was put in the centre of the plot area (Figure 5 c). The position of the frame was marked to make sure observations were done in more or less the same spot each round. Each phenophase for each species was assessed at the level of sub-square, where the most advanced phenophase was registered. Each species had 4-6 pre-defined phenophases for

reproductive and vegetative development (Appendix, Table 1). Reproductive phenology for *S. polaris* was registered for male and female flowers separately. Note that some species had already passed the first phenophases at the start of the data collection, while others did not reach their final phenophase before the end of the data collection period. Hence, the complete phenological succession of all species was not captured.

Statistical analysis

To test for treatment effects on plant phenology, we first estimated the time at which each phenophase was reached for each treatment (referred to as timing of phenophase), using linear mixed effect models at the square level (i.e. the 16 sub-squares within each plot, see Figure 4). Treatment and natural icing was set as the only explanatory variables, including plot nested in block as random factors. This was done separately for each phenophase of each species. Models including natural ice thickness as explanatory variable was also tested, however the effect was only statistically significant (positive) for *S. polaris* (male flower) in reaching phenophase 3. Thus, this covariate was excluded for simplicity.

In some cases, a species did not reach its final phenophase within the last day of observations. To avoid the potential bias in treatment effect size due to this, we performed a parallel analysis adding a fictive observation of the final phenophase to day 56, that is, a likely day for the next round of observations if the field work had continued (the last day of observations was day number 51). This parallel approach thus assumes that all squares would have reached the final phenophase five days after the fieldwork ended. Cases of which species missed sufficient data registrations for the first phenophases were removed from the analysis.

To get additional insight to the phenological advancement/delay due to treatments, we estimated the phenophase reached in the first round of observations in early summer and the rate of phenological development simultaneously, by fitting a species-specific development curve at the plot level. The nlme package in R (Pinheiro et al. 2016) was applied to fit a sigmoid curve to the data for each plot and species separately, using non-linear least square regression. This was done applying the 3-parameters logistic function to phenophase y:

$$y = \frac{a}{1+be^{-\mathrm{cx}}} \qquad (1)$$

where *a* represents the asymptote (fixed to the species-specific last phenophase), *b* defines the value of the intercept as *a* / (1+*b*), and *c* is the slope of the curve at time x = 0 (Crawley 2007), where the first day of data collection is set to day 0. In this model, *b* is inversely related to the phenophase (compared to the final phenophase) reached by a species at day 0. Thus, a higher *b* value indicates a less advanced phenophase at day 0. The higher the *c*-value, the higher is the rate of phenological development. That is, the estimated curve reflects the change in phenophase in a given plot with time. Once estimated, the *b* and *c* parameters where used as response variables in mixed-effect models, where treatment was set as fixed effect and block as a random effect. For vegetative phenology (*S. polaris* and *B. vivipara*), all plots in all treatments were recorded to be in the same phenophase (y = 3) for the first five rounds of observation. Round six (10th of July) was hence set to day 0. Furthermore, the first round of observations for the graminoids' reproductive phenology was removed to avoid bias due to missing data for most plots. This might be explained by individuals being underdeveloped and so tiny that they were overlooked during observations.

To investigate whether phenology at the first day of observations (*b*) and the rate of development (*c*) differed between treatments (and whether this depended on species), we analysed *b* and *c* separately, using the lme4 package in R (Bates et al. 2016). Since the individual species has different scales of phenological development, where phenological phases have different meaning depending on species, *b* and *c* were first standardized within species by:

$$x_{new} = \frac{x - \mu}{\sigma} \quad (2)$$

For *b* and *c* estimates of a given species, *x* is the original estimate, μ is the sample mean and σ is the standard deviation. This is to make the phenology of the different species comparable, with a mean of zero and a variance of 1 (Milligan and Cooper 1988). To weight for the plot-specific uncertainties, b/c estimates were weighted with 1/SE in the model. Standard errors (SEs) were first normalized (scaled) within species (with mean = 0.5) to avoid problems with dividing one by zero (Basheer and Hajmeer 2000). This is to avoid that species with generally small *b* and *c* estimates, and hence small SE estimates, were given more weight than those with larger *b* and *c* estimates, and hence larger SEs.

The following explanatory variables were included in a global model; species, treatment, natural ice thickness and the interaction species×treatment, with plot nested in block as random factors (i.e. random intercept). Model selection was performed using an information theoretic

approach by means of the Akaike Information Criteria corrected for small sample sizes (AICc) (Burnham and Anderson 2002), applying the MuMIn package (Barton 2016). AIC_C weight was also applied, which indicates the probability that a given model is the best model for the observed data (Burnham and Anderson 2002).

The total number of candidate models was ten for both *b* and *c*, in both the vegetative and reproductive category. Model selection was based on models fitted with maximum likelihood technique (ML). The model with $\Delta AICc = 0$ is perceived to have the best support in the data and models with $\Delta AICc < 2$ are considered to have substantial support from the data, in relation to the candidate models (Burnham and Anderson 2002). Parameter estimates were obtained from models fitted with REML (Bates 2014).

Note that natural ice thickness, which was measured at the time of the icing treatment in February (plot mean = 0.9 cm, SD = 1.2 cm, min = 0 cm, max = 5.2 cm), did not differ significantly among treatments, based on model selection of linear mixed models with plot nested in block as random effects. The AICc for the model including treatment as explanatory variable was 130.06, while AICc for the model including only the intercept was 124.32 (model results not presented).

All statistical analyses were done using the software R version 3.2.2 (R Core Team 2016).

Results

Timing of phenophases

The analyses of timing of reproductive phenophases (i.e., the estimated day of reaching a given phenophase) showed an overweight of positive estimates (14 out of 21) in the icing treatment across species (i.e., phenophases were reached later than control plots). This amount is not higher than expected by chance ($\chi^2 = 1.71$, df = 1, P = 0.19), but half of the positive estimates were statistically significant, while no negative estimates were significantly different from zero (Appendix, Table 2). This suggests support for an overall positive (delaying) effect of icing, however with small effect size and large variation between species and phenophases. Both the warming treatment and the combined icing and warming treatment had more negative estimates (20 out of 23 and 19 out of 23, respectively) than expected by chance ($\chi^2 = 11.13$, df = 1, P < 0.001 and $\chi^2 = 8.52$, df = 1, P < 0.01 for W and IW, respectively) (i.e., phenophases were reached earlier than controls). Generally, the effect of the combination of warming and icing on timing of phenophases seemed to be intermediate between the effect of icing and the effect of warming (except for the timing of phenophase 5 for the female flower of *S. polaris*, which was earlier in the IW treatment than in W, see Appendix, Table 2). That is, the reproductive phenology of species in the combined warming and icing treatment seemed in general to be more advanced than for species in the icing treatment, but less advanced than for species in the warming treatment, on an overall basis (Table 2 in Appendix; Figure 7). However, there was large variation in estimated treatment effect across species and specific phenophases, where the timing of phenophases in the icing treatment was between (mean ± SE) -3.60 ± 4.26 to 3.86 ± 1.09 days different from control. Overall, the icing treatment seemed to have slightly later timing of the early phenophases, but to a lesser degree for later phases (Appendix, Table 2). Plots with experimental ice melted on average ca three days later than plots without experimental ice, but the delay was not statistically significant based on a mixed linear model with plot nested in block as random effect (2.84 (mean) ± 2.76 (SE), t = 1.03, p = 0.34). Thus, phenology in the icing treatment were not more delayed than the time delay of ice melting. The timing of phenophases in the warming treatment was between (mean ± SE) -7.94 ± 3.12 to 0.82 ± 2.01 days different from control, and the timing of phenophases in the combined icing and warming treatment was between (mean ± SE) -11.17 ± 2.92 to 1.27 ± 3.40 days different from control (Appendix, Table 2). The warming treatment and the combined icing and warming treatment generally appeared to have largest effect on later phenophases (Table 2 in Appendix; Figure 7, b, d, f, h, j, l).

For vegetative phenology of both *B. vivipara* and *S. polaris*, there was no significant or tendency for consistent differences between the treatments and the control in the day phenophases were reached (Table 3 in Appendix; Figure 8 b, d).

Early phenology

For reproductive phenology, both treatment and natural ice thickness were estimated to have an effect on the phenophases registered at the first day of observations, as indicated by the model selection (Appendix, Table 4 A, Model 1). This was general for all species, because including species as explanatory variable did not improve the model (Appendix, Table 4 A, Model 3). These results suggest that the warming treatment and the combined icing-warming treatment induced a more advanced phenology at day 0 (first day of observations) than in the control treatment (Appendix, Table 4 A, Model 1). The estimate of the icing-treatment effect was positive but uncertain, while natural ice thickness caused a delay in phenology (positive estimate; Appendix, Table 4 A, Model 1).

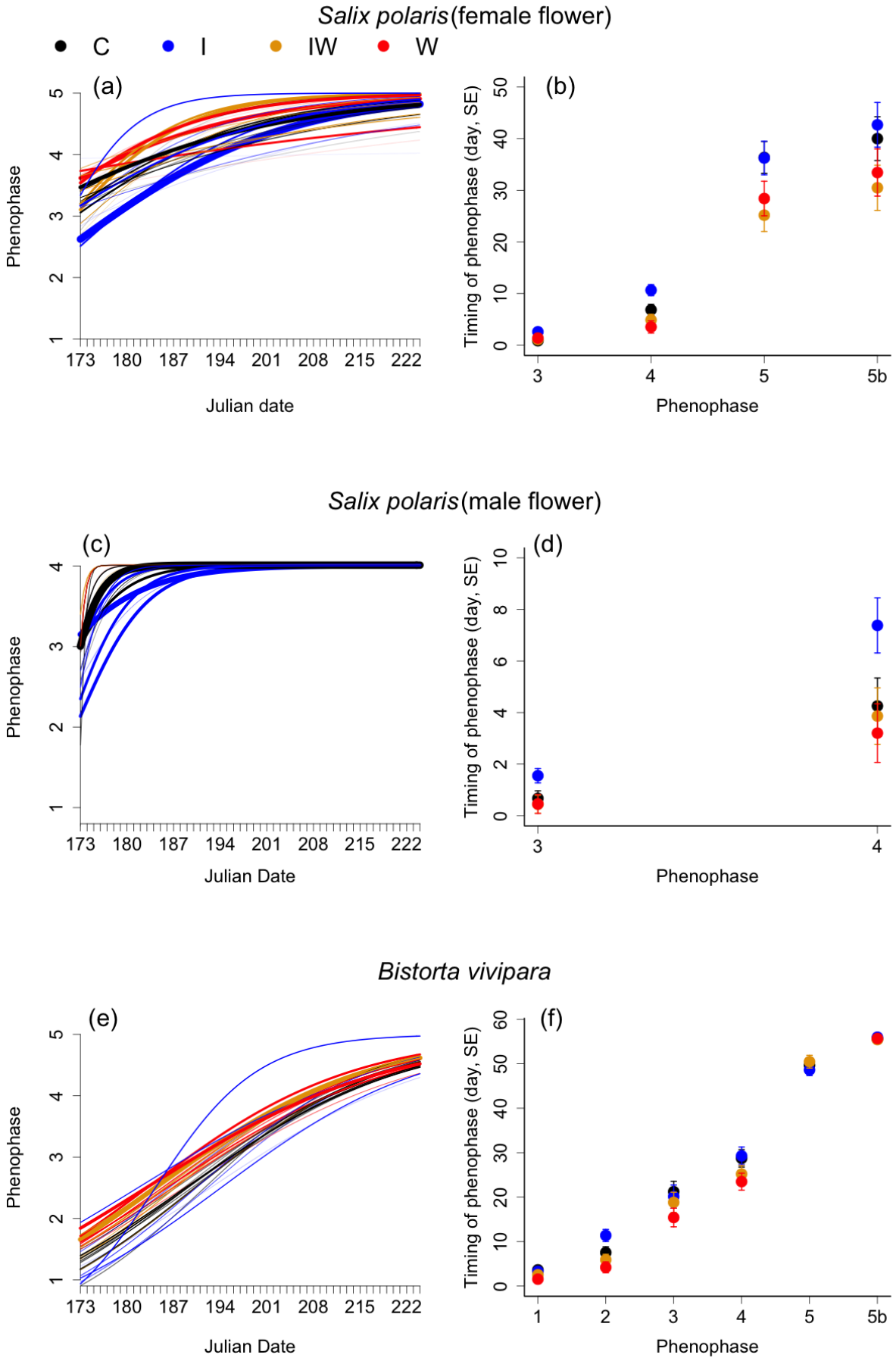
For vegetative phenology, we found no effect of treatment, species or natural ice thickness on early phenology (Appendix, Table 4 C, Model 1). Models containing natural ice thickness, treatment and species as explanatory variables were not better than the model including only the intercept (see Appendix, Table 4 C). These results suggest that the treatments had in fact a limited effect on the estimated vegetative phenophase at the first round of observations (intercept ± SE = -0.06 ± 0.19).

Rate of phenological development

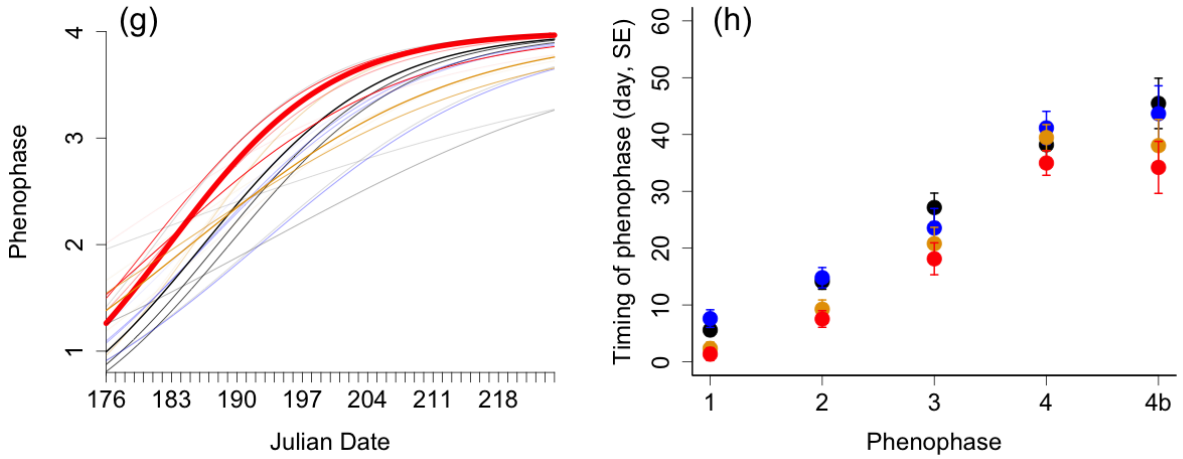
The rate of phenological development, for reproductive phenology was best explained by a model including only natural ice thickness (positive effect, i.e. faster developmental rate) as explanatory variable (Appendix, Table 4 B, Model 1). The model with only the intercept, and the model including treatment as explanatory variable also had ΔAIC_C values below 2 and should therefore also be considered. However, these models had a relative low AICc-weight

and the estimates were uncertain for all treatments (Appendix, Table 4 B, models 2 and 3).

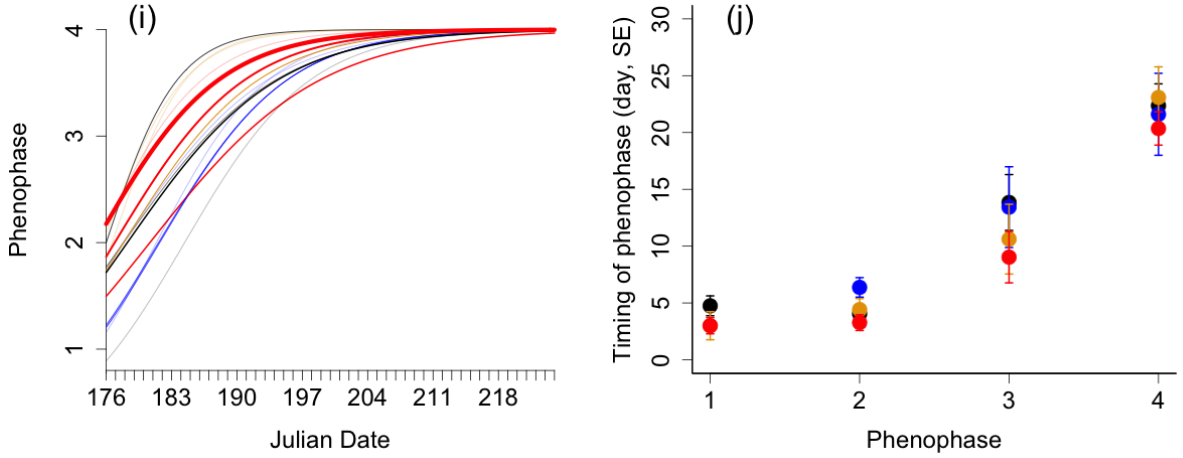
Neither treatment, species nor natural ice thickness were included in the top ranked model of developmental rate in vegetative phenology (see Appendix, Table 4 D, Model 1). The model including natural ice as explanatory variable (positive effect) had $\Delta AIC_C < 2$ and should be considered, however the parameter estimate was uncertain and the AIC-weight was relatively low (see Appendix, Table 4 D, Model 2). Nevertheless, these results indicate no evidence for treatment effects on the rate of vegetative phenological development.


Salix polaris (female flower)
C
I
IW
W
(a)
Phenophase
Julian date
(b)
Timing of phenophase (day, SE)
Phenophase
Salix polaris (male flower)
(c)
Phenophase
Julian Date
(d)
Timing of phenophase (day, SE)
Phenophase
Bistorta vivipara
(e)
Phenophase
Julian Date
(f)
Timing of phenophase (day, SE)
Phenophase

Poa Arctica



Alopecurus Borealis



Luzula confusa

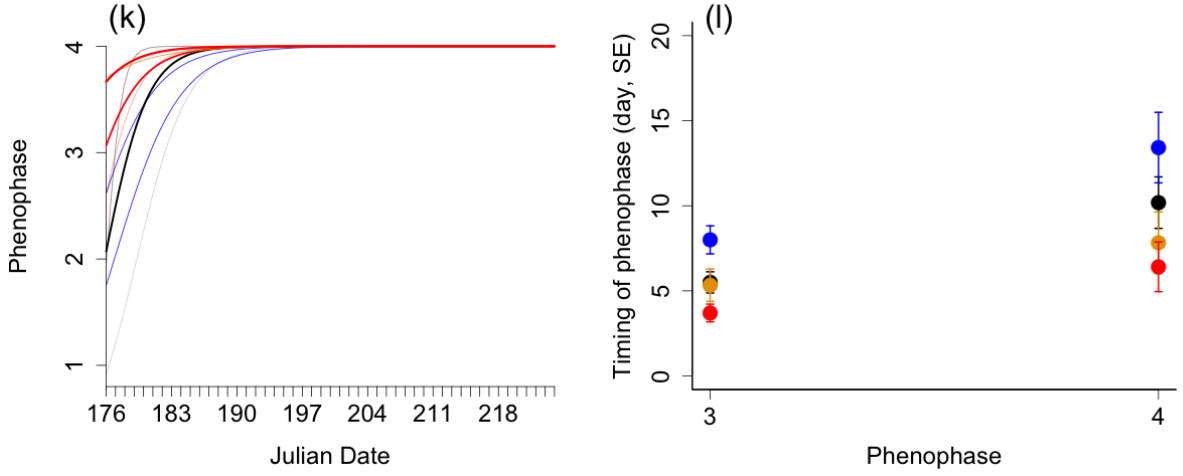


Figure 7: Plot-wise nonlinear curve fitting of phenological development (a, c, e, g, i, k) and estimated day of observations for reaching a specific phenophase (b, d, f, h, j, l) during summer 2016, for reproductive phenology (see Appendix, Table 1 for description of phenophases). Day 0 = Julian date 173 (22th of June) for all species, expect for the graminoids, where day 0 = Julian date 176 (25th of June). To account for sample size, the thickness of the lines is proportional to the number of the respective species' flowers present in the plots. Phenophases marked with the letter b represents the parallel analysis for cases where a species did not reach its final phenophase within the last day of observations. The timing of this phenophase was hence set to a fictive day 56, assuming that the species would have reached their final phenophase within this day, as explained in the method section. The different colours each represent a treatment. C = control (black), I = icing (blue), IW = icing and warming (orange) and W = warming (red).

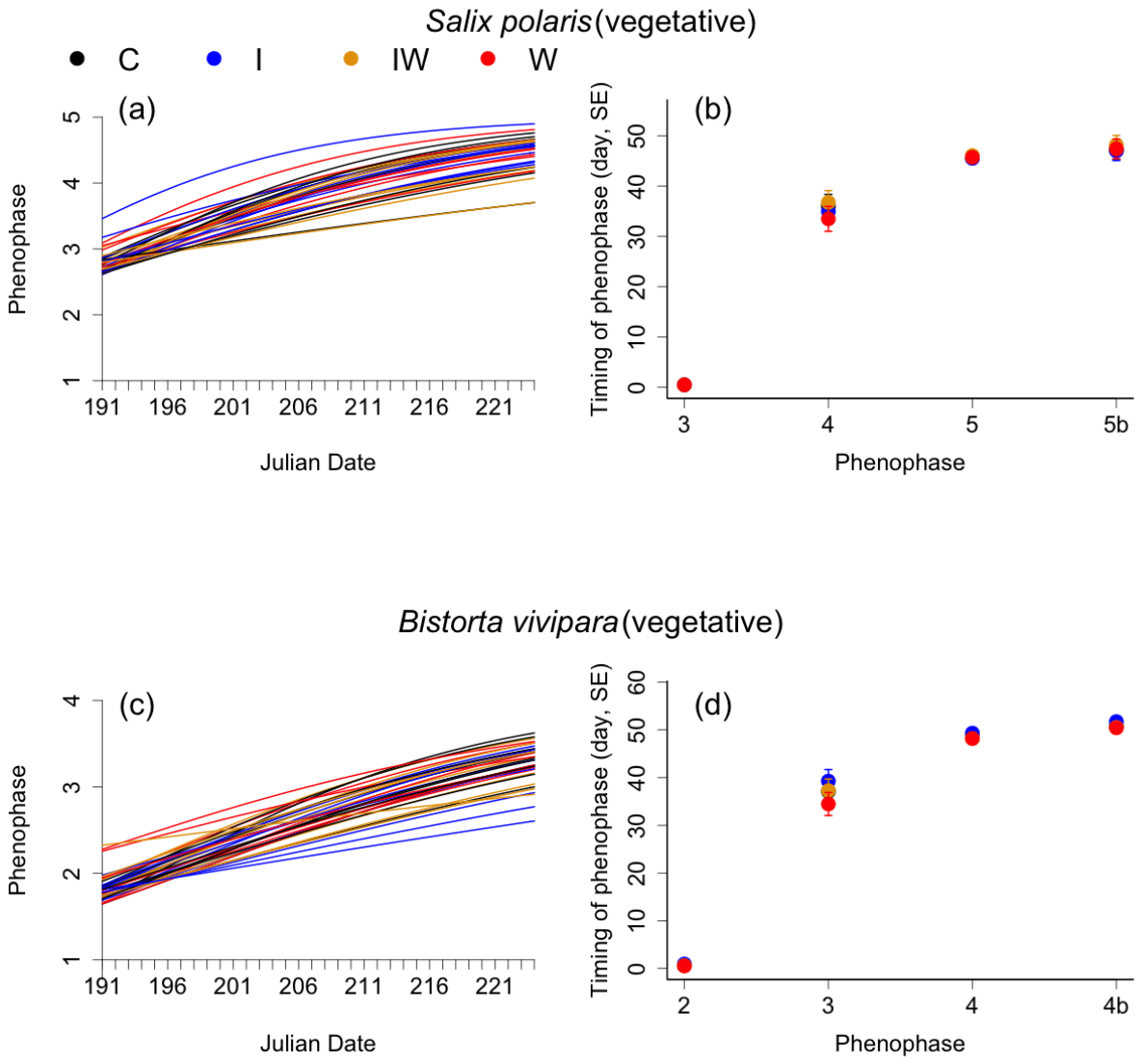


Figure 8: Plot-wise nonlinear curve fitting of phenological development (a, c) and estimated day of observation for reaching a specific phenophase (b, d) during summer 2016, for vegetative phenology (see Appendix, Table 1 for description of phenophases). Day 0 = Julian date 191 (10th of July). Phenophases marked with the letter b represents the parallel analysis for cases where a species did not reach its final phenophase within the last day of observations. The timing of this phenophase was hence set to a fictive day 56, assuming that the species would have reached their final phenophase within this day, as explained in the method section. The different colours each represent a treatment. C = control (black), I = icing (blue), IW = icing and warming (orange) and W = warming (red).

Discussion

In the present experimental study, we investigated potential effects of climate change on reproductive and vegetative phenology of key Arctic tundra plant species. This was done by experimentally simulating ground ice formation due to heavy ROS events in winter and increased summer temperatures (applying OTCs). Across species, the results suggest that the icing treatment tended to delay reproductive phenology. Both warming and the combination of icing and warming advanced reproductive phenology through the growing season, with stronger effect on later phenophases. Further, the effect of the combined treatment was generally in between the effect of the warming and icing treatment. We found no treatment effect on vegetative phenology across species.

The ice-induced delay in phenology due to delayed melting found in the present study, is consistent with other studies on the effect of later snow melt in spring, where these results also reported delayed phenological development in Arctic plant species (Wipf and Rixen 2010, Cooper et al. 2011). Furthermore, the delay in reaching the early to middle phenophases (typically flower development phenophases) seemed to be greater than the delay in reaching later phases (seed maturation and flower senescence). Although, it was uncertain whether the icing treatment caused a change in phenological developmental rate compared to control plots (Appendix, Table 4 B, Model 3), this could indicate a catch-up effect through the season. This is supported by Cooper et al. (2011), who found that some Arctic plant species responded to later spring onset (due to later snow melt) by accelerating their development through the season. Furthermore, late phenophases may also be triggered by seasonal changes in light and photoperiod (Arft et al. 1999, Cooper et al. 2011), which could counteract impacts of ice encasement (Preece and Phoenix 2014). Also, the thickness of natural occurring ice showed a tendency in increasing the phenological development rate, although, this could also be due to other plot environmental differences not accounted for in this study. However, our results are inconsistent across species and phenophases, and the icing treatment caused only a slight delay (~three days) in melting time, which hence give a small effect size. In addition, snow and ice has different physical properties (Pomeroy and Brun 2001), in regards to gas permeability and insulating effect, which may affect physiological processes in plants (Gudleifsson 1997, Albert and Perron 2000, Preece and Phoenix 2014). Thus, whether results from studies on delayed snowmelt are comparable to our study is questionable.

Another question of interest is whether the icing treatment has an effect on phenology beyond the delay in ice melting time. As expected, the icing treatment caused a delay in the timing of melting processes, and melted on average three days later than control plots. The longest estimated delay in reaching a specific phenophase seen in the icing treatment is approximately four days for *B. vivipara* in reaching phenophase 2 (Appendix, Table 2). Thus, our results do not indicate that the icing treatment has an additional effect on phenology other than delaying the initiation of spring. This agrees with Preece et al. (2012), who found that sub-Arctic species were relatively tolerant to icing, considering phenology, growth and physiology. Furthermore, Arctic plant species have shown a fairly high anoxia tolerance (Crawford et al. 1994), which plants can be exposed to during ice encasement (Preece and Phoenix 2014). However, responses to environmental disturbances may be slow in long lived, slow-growing perennial species (Arróniz-Crespo et al. 2008). There may also be a lag in responses due to pre-formation of flower buds one to several seasons prior to flowering (Sørensen 1941, Diggle 1997, Arft et al. 1999). This means that some treatment effects may not occur with only a one-year experiment.

Sexual reproduction is important for maintenance of genetic diversity. This plays a critical role for plants' ability to adapting to changing climatic conditions and hence the future viability of Arctic plant populations (Jonsdottir 2011). The frequency of plant establishment following seed germination in the harsh Arctic climate conditions are fairly low (Bliss 1971, Jonsdottir 2011, Müller et al. 2011). Consequently, a shorter growing season due to later melting in spring could have negative effects on the rate of sexual reproduction and reproductive success in Arctic plant species (Bliss 1971, Cooper et al. 2011, Jonsdottir 2011). Therefore, the advantage of advanced flowering may be especially important for late flowering species like *P. arctica* and *A. borealis* with low seed set. A shorter growing season and delayed phenology could hence be extra critical, considering reproductive success for these species (Molau 1993). However, the small delay in ice melt seen in our study may not have a considerable effect. Still, a longer delay could occur under circumstances with an even thicker ice layer than the 13 cm in our experiment, as ROS can result in ground-ice layers up to a thickness of 20 cm (Hansen et al. 2014). Further, our results indicate that phenology of the graminoids (*P. arctica, A. borealis* and *L. confusa*) seems to be less delayed by the icing treatment than the dwarf shrub *S. polaris* (Table 2 in Appendix; Figure 7). This is consistent with a review done by (Wipf and Rixen 2010) on Arctic snow manipulation experiments, where the results suggest that phenology of graminoids responds less to changes in melting time than the phenology of dwarf shrubs. Further investigation of seed viability and germinability could give better insight to any

potential additional effects of ground icing on reproductive success in high Arctic tundra species.

As expected, the warming treatment advanced reproductive phenology across all species, which agrees with several studies (Wookey et al. 1993, Arft et al. 1999, Cleland et al. 2007, Høye et al. 2007). Our results match the findings of The International Tundra Experiment (ITEX) (Arft et al. 1999), where warmer temperatures advanced flowering phenology. Still, we found no difference in phenological developmental rate in warmed plots compared to controls. However, considering that the warming treatment is having a particular effect on later phenophases involving flower development and seed maturation (Table 2 in Appendix; Figure 7 b, d, f, h, j, l), this could indicate that the developmental rate is increasing through the season. Note however that the air and soil temperatures inside the OTCs were in average only 0.85 °C and 0.98 °C higher, respectively, than in control plots. This is considerably less than the average increase of 1.2 – 1.8 °C and up to 5.2 °C for air and soil temperature, respectively, found when testing the efficacy of OTCs in Arctic areas (Marion et al. 1997). The relatively low temperature raise seen in our OTCs, might be explained by an overall cloudy summer, with low solar radiation. This could result in a lower phenological advancement than in summers with less cloudiness and hence larger temperature increase, as growth rate in Arctic plant species may be limited by temperature (Chapin III 1983).

For Arctic plants in general, we expect that advanced reproductive phenology is an advantage and that warmer summers enhance successful reproduction (Wookey et al. 1995). Thus, the sooner Arctic plants reach their reproductive phenophases, the greater the probability of producing viable offspring. However, increased temperatures might not be beneficial for all species. A study by Chapin and Shaver (1996) found that advanced phenology, as a response to increased temperature, may cause a depletion of stored plant reserves in Arctic species. Increased temperatures could therefore result in a changed species composition, in favor of fast growing species able to preserve their nutrient uptake (Chapin et al. 1996). In addition, accelerated time of flowering can cause trophic mismatches where flowering could be ahead of pollinators. This could result in lower seed production due to a lower rate of pollination (Kudo and Ida 2013).

The combined warming and icing treatment also advanced phenology across species. We expected the phenology of species in this treatment to be initially delayed due to later melting,

and increasing the developmental rate through the season due to increased temperatures. However, the first observed phenophases appear earlier than in control plots (Table 2 in Appendix; Figure 7 b, d, f, h, j, l) but, as our measurements missed the initial phenophases, we cannot rule out a possible delay earlier in the season due to the icing effect. Overall, the effect of the combined icing - warming treatment indeed seems to be in between the effect of the icing and warming treatments alone (Table 2 in Appendix; Figure 7). That is, phenology is more advanced in the combined treatment than in the icing treatment, but less advanced than the phenology in the warming treatment. This could indicate that warmer summer temperatures may outweigh potential negative effects of late spring onset. This might be explained by plants being well adapted to utilize warmer conditions (Chapin III 1983, Korner and Diemer 1987). The combined treatment effect seems to be stronger on phenophases later in season, although not reaching the same extent as the effect of the warming treatment.

We found no significant treatment effect on vegetative phenology (Table 3 in Appendix; Figure 8). This implies that warming or icing neither advances nor delays vegetative phenology in the observed phenophases. This could be explained by Arctic plants being well adapted to the highly variable Arctic summer weather conditions (Jónsdóttir 2005). No conclusion can be drawn on treatment effect on the first phenophases, however, as they were missed under field work. In agreement with Arft et al. (1999), our analysis shows that the final phenophases were reached at approximately the same time (Table 3 in Appendix; Figure 8 b, d), suggesting that senescence might be triggered by a declining photoperiod (Borner et al. 2008). However, there is disagreement whether increased temperatures delays or advances autumn leaf senescence in Arctic vegetation. For example, Cooper (2014) suggests based on a literature review that senesces happens earlier with warmer temperatures due to increased respiration. Conversely, a study by Marchand et al. (2004) reports that senescence in high Arctic tundra is postponed by higher temperatures.

Overall, the results discussed here display large variation between species and phenophases, which might be explained by the species' different reproductive, morphological-, and physiological characteristics (Billings 1992). In addition to small scale spatial heterogeneity, the sample size is fairly low, both in terms of the number of experimental units (plots) and the absence of some species (especially *A. borealis* and *L. confusa)* in some plots (Appendix, Table 5). Furthermore, as we missed early phenophases of bud burst as well as the final phenophases for most species in this study, it is not possible to compare the effect of treatments across the

full range of phenological development. Consequently, the analytic approach regarding the estimates from the nonlinear curve fitting analysis might not capture the treatment effect well. It is hence questionable whether the effects are presented in the most realistic way. For instance, the analysis of phenology at the start of observations resulted in uncertain estimates for the icing treatment, despite that the analysis of phenophase timing revealed an overall delay. However, the estimated curves support the inference that the icing treatment had an overall tendency to delay reproductive phenology, and that reproductive phenology of species treated with warming and the combination of icing and warming is more advanced compared to control plots over the season (Figure 7 a, c, e, g, i, k). Hence, to increase the quality (in regards to species abundance) and number of experimental units may be recommended for future studies. In addition, field work should start earlier in spring and last throughout the growing season to capture the full phenological development. It should also be taken into account that the winter (2015/2016) of the experimental setup had considerable amounts of natural ice covering the ground. As the analysis reveals, natural ice thickness causes an additional delay in phenology. This could indicate that the natural ice occurring in the plots, to some degree weakened or reduced the magnitude of treatment effects. In addition, the mean spring temperature was generally high the year the fieldwork was conducted, compared to previous decades (Figure 2). This could also influence spring onset (Høye et al. 2007). Also, the level of soil moisture and nutrient availability can affect phenological responses (Walker et al. 1995). However, we did not measure or account for these environmental covariates in this study.

The evident responses to climate change related experimental disturbance and large variability within species and taxa illustrate that biological interactions in Arctic areas are easily disturbed (Høye et al. 2007). Phenological shifts can therefore be dramatic for these ecosystems and may disturb trophic interactions and affect reproductive success (Høye et al. 2007). This can for instance be a mismatch in the peak of resource quality and the peak of herbivore demand in the reproductive period (Post and Forchhammer 2008), as Arctic plants reach a peak of nutrient quality soon after emergence in spring (Klein 1990). Consequently, this can lead to higher offspring mortality (Post and Forchhammer 2008). Based on our results for these important forage species, it might be of importance to investigate if phenological shifts are causing trophic mismatches also in Svalbard. Given the predicted increase in Arctic winter rain events (Hansen et al. 2014), and the importance of vegetation phenology, structure and productivity for both resident and migratory herbivores, understanding how tundra vegetation responds to icing is also fundamental for our understanding of future ecosystem-level changes.

As the first study investigating the effect of ground ice formation on phenology in high Arctic plant species, this study suggests that changes in climate can cause changes in phenology, both as a result of later melting due to ground ice formations and warmer summer temperatures. This could possibly have implications for reproductive success in some plants, species compositions and higher trophic levels (Bliss 1971, Chapin et al. 1996, Høye et al. 2007, Post and Forchhammer 2008, Iversen et al. 2009, Cooper et al. 2011, Jonsdottir 2011, Kudo and Ida 2013). In addition to the need for a longer study period to detect possible delayed plant responses, or effects of repeated years of treatment, further investigations on other plant traits, such as seed germinability, and reproductive success could help increase our understanding of the potential consequences of phenological shifts, in response to future changes in winter climate and increased temperatures.

Acknowledgements

This master thesis was written at the Centre for Biodiversity Dynamics (CBD) as a part of my teacher education at the Norwegian University of Science and Technology (NTNU). Fieldwork was made possible by additional funding from Kong Haakon the 7th education fund for Norwegian youths and Jan Christensens legate, as well as the University Centre in Svalbard (UNIS).

I would like to thank my excellent team of supervisors Christophe Pelabon and Brage Bremset Hansen at NTNU and Ingibjörg Svala Jónsdóttir UNIS. I am very grateful for all your time spent in guiding me through this process. I am thankful for the opportunity I got to take part in this project and to participate in the fieldwork at Svalbard. It has truly been an educational experience. Thanks to Bart Peeters for great help with R-problems.

Thanks to Ingibjörg Svala Jónsdóttir and Matteo Petit Bon for excellent guidance during fieldwork and thanks to all field assistance contributing to the fieldwork. A special thanks to my volunteering field assistant, tour guide and entertainer Gaute Heggvold, and a great thanks to Hanne Haraldsen, Marta Grotheim and Hanna Sørhus for good times, both in field and in the NTNU-cabin.

I must also thank my fellow students at LUR and finally, a special thanks to my good friend Ragnhild Christine and my family for great moral support and motivation.

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Appendix

Table 1: Description of the study species specific phenophases for reproductive and vegetative phenology. Based on the ITEX manual (Molau and Mølgaard 1996), modified by I.S. Jónsdóttir.

		Phenophase						
Phenology	**Species**	**0**	**1**	**2**	**3**	**4**	**5**	**6**
Reproductive	*S. polaris* ♀	No flowers visible	Flowers visible	Stigmas visible	Stigmas receptive	Stigmas withered	Capsules open, seed dispersed	
	S. polaris ♂	No flowers visible	Flowers visible	Anthers visible	Pollen released	Anthers withered		
	B. vivipara	No flower buds visible	Visible inflorescence in sheath	Inflorescence stretched out of sheath	Bulbils developing	Bulbils started to shed	All bulbils shed	
	Graminoids	Inflorescence not visible	Inflorescence visible, but not stretched	Inflorescence stretched and first flowers open	Stigmas receptive (white and showy)	Stigmas withered	Seed mature, i.e. utricle (*perigynium*) filled	Seed shed
Vegetative	*S. polaris*	Buds closed	Bud burst, but leaves not exposed	Leaf not yet unfurled	Leaf fully expanded/mature	Leaf starting to senescence (yellow spotting)	Leaf fully senescent (yellow)	
	B. vivipara	No new leaves visible	First leaf visible, still rolled	First leaf unrolled	First colour change (redish)	Leaves withered		

Table 2: Timing of phenophases for reproductive phenology. The estimated day of observations ± SE species reached their respective phenophases in a given treatment. The first day of observations is set to day 0, and the last day of observations is day 51. In cases where species did not reach its final phenophase within the last day of observations, this was set to a fictive day 56, assuming that the species would have reached their final phenophase within this day, as explained in the Methods section. Phenophases which fall under this category is marked with the letter b. Estimates for I, IW and W, are relative to control, where Intercept = control, I = icing treatment, IW = combined icing and warming treatment, W = warming treatment and Phase = phenophase reached. Blank cells indicate missing data.

Species	**Phase**	**Intercept (C)**	**I**	**IW**	**W**
***S. polaris* (female)**	3	0.86 ± 0.38, t = 2.269, p < 0.05	**1.74 ± 0.55, t = 3.19, p < 0.01**	0.26 ± 0.58, t = 0.45, p = 0.65	0.53 ± 0.63, t = 0.85, p = 0.41
	4	6.85 ± 1.07, t = 6.41, p < 0.001	**3.80 ± 1.26, t = 3.03, p < 0.01**	-1.96 ± 1.27, t = -1.54, p = 0.14	**-3.32 ± 1.35, t = -2.47, p < 0.05**
	5	36.35 ± 3.08, t = 11.79, p < 0.001	-0.10 ± 3.01, t = -0.03, p = 0.97	**-11.17 ± 2.92, t = -3.83, p < 0.01**	**-7.94 ± 3.12, t = -2.55, p < 0.05**
	5b	40.0 ± 4.25, t = 9.42, p < 0.001	2.68 ± 3.87, t = 0.69, p = 0.50	**-9.51 ± 3.91, t = -2.44, p < 0.05**	-6.56 ± 4.10, t = -1.6, p = 0.12
***S. polaris* (male)**	3	0.67 ± 0.29, t = 2.31, p = 0.051	**0.88 ± 0.37, t = 2.35, p < 0.05**	-0.23 ± 0.43, t = -0.54, p = 0.60	-0.22 ± 0.44, t = -0.49, p = 0.63
	4	4.26 ± 1.09, t = 3.92, p < 0.05	**3.12 ± 0.78, t = 4.01, p < 0.001**	-0.39 ± 0.81, t = -0.48, p = 0.64	-1.05 ± 0.87, t = -1.21, p = 0.24
B. vivipara	1	3.63 ± 0.68, t = 5.36, p < 0.001	-0.35 ± 1.01, t = -0.34, p = 0.74	-1.11 ± 0.99, t = -1.12, p = 0.27	**-2.10 ± 1.05, t = -2.0, p = 0.057**
	2	7.52 ± 1.31, t = 5.76, p < 0.01	**3.86 ± 1.09, t = 3.54, p < 0.01**	-1.62 ± 0.94, t = -1.73, p = 0.1	**-3.33 ± 0.92, t = -3.61, p < 0.01**
	3	21.2 ± 2.31, t = 9.20, p < 0.001	-1.10 ± 2.95, t = -0.37, p = 0.71	-2.41 ± 2.68, t = -0.90, p = 0.39	**-5.82 ± 2.51, t = -2.32, p < 0.05**
	4	28.73 ± 1.96, t = 14.66, p < 0.001	0.56 ± 1.56, t = 0.36, p = 0.72	**-3.53 ± 1.47, t = -2.40, p < 0.05**	**-5.24 ± 1.45, t = -3.61, p < 0.01**
	5	49.65 ± 1.46, t = 34.04, p < 0.001		-1.036 ± 1.88, t = -0.55, p = 0.60	0.82 ± 2.01, t = 0.41, p = 0.70
	5b	55.58 ± 0.23, t = 236.95, p < 0.001	0.41 ± 0.34, t = 1.19, p = 0.24	-0.14 ± 0.30, t = -0.45, p = 0.66	0.10 ± 0.30, t = 0.33, p = 0.75
P. arctica	1	5.59 ± 0.99, t = 5.62, p < 0.001	2.01 ± 1.84, t = 1.09, p = 0.29	**-3.24 ± 1.51, t = -2.16, p = 0.051**	**-4.24 ± 1.51, t = -2.80, p < 0.05**

	2	14.15 ± 1.38, t = 10.23, p < 0.01	0.66 ± 1.68, t = 0.39, p = 0.70	**-4.88 ± 1.53, t = -3.18, p < 0.01**	**-6.61 ± 1.34,t = -4.95, p < 0.001**
	3	27.15 ± 2.53, t = 10.72, p < 0.001	-3.60 ± 4.26, t = -0.85, p = 0.41	-6.36 ± 3.83, t = -1.66, p = 0.11	**-9.02 ± 3.78, t = -2.39, p < 0.05**
	4	38.19 ± 2.52, t = 15.15, p < 0.001	2.97 ± 3.86, t = 0.77, P = 0.45	1.27 ± 3.40, t = 0.37, p = 0.72	-3.21 ± 3.32, t = -0.96, p = 0.36
	4b	45.47 ± 4.43, t = 10.26, p = 0.005	-1.80 ± 3.46, t = -0.52, p = 0.613	**-7.42 ± 3.04, t = -2.44, p = 0.04**	**-11.26 ± 3.00, t = -3.75, p < 0.01**
A. borealis	1	4.88 ± 0.89, t = 5.46, p = 1		-1.9 ± 1.54, t = -1.24, p = 1	-1.88 ± 1.15, t = -1.63, p = 1
	2	4.04 ± 0.72, t = 5.60, p < 0.05	**2.33 ± 0.76, t = 3.07, p < 0.01**	0.38 ± 0.84, t = 0.45, p = 0.66	-0.77 ± 0.53, t = -1.44, p = 0.16
	3	13.84 ± 2.46, t = 5.64, p < 0.01	-0.41 ± 3.63, t = -0.11, p = 0.91	-3.23 ± 3.08, t = -1.048, p = 0.31	**-4.81 ± 2.34, t = -2.054, p = 0.06**
	4	22.36 ± 1.92, t = 11.64, p < 0.001	-0.76 ± 4.09, t = -0.19, p = 0.85	0.72 ± 3.31, t = 0.22, p = 0.83	-2.01 ± 2.42, t = -0.83, p = 0.43
L. confusa	3	5.50 ± 0.62, t = 8.83, p < 0.001	**2.5 ± 1.03, t = 2.42, p <0.05**	-0.17 ± 1.14, t = -0.15, p = 0.88	**-1.80 ± 0.81, t = -2.22, p < 0.05**
	4	10.19 ± 1.51, t = 6.73, p < 0.05	3.24 ± 1.97, t = 1.65, p = 0.11	-2.36 ± 1.51, t = -1.56, p = 0.12	**-3.77 ± 1.10, t = -3.43, p < 0.01**

Table 3: Timing of phenophases for vegetative phenology. The estimated day of observations ± SE species reached their respective phenophases in a given treatment. The first day of observations is set to day 0, and the last day of observations is day 51. In cases where species did not reach its final phenophase within the last day of observations, this was set to a fictive day 56, assuming that the species would have reached their final phenophase within this day, as explained in the Methods section. Phenophases which fall under this category is marked with the letter b. Estimates for I, IW and W, are relative to control, where Intercept = control, I = icing treatment, IW = combined icing and warming treatment, W = warming treatment and Phase = phenophase reached.

Species	**Phase**	**Intercept (C)**	**I**	**IW**	**W**
S. polaris	4	35.98 ± 2.36, t = 15.26, p < 0.001	-1.054 ± 1.75, t = -0.60, p = 0.55	0.76 ± 1.76, t = 0.43, p = 0.67	-2.51 ± 1.89, t = -1.33, p = 0.20
	5	45.56 ± 0.84, t = 54.02, p < 0.001	-0.04 ± 0.81, t = -0.05, p = 0.96	0.50 ± 0.83, t = 0.60, p = 0.55	0.16 ± 0.86, t = 0.18, p = 0.86
	5b	47.18 ± 1.94, t = 24.37, p < 0.001	-0.19 ± 1.08, t = -0.17, p = 0.86	0.96 ± 1.08, t = 0.89, p = 0.38	0.20 ± 1.16, t = 0.17, p = 0.87
B. vivipara	2	0.63 ± 0.19, t = 3.34, p < 0.01	0.33 ± 0.27, t = 1.23, p = 0.24	-0.01 ± 0.27, t = -0.05, p = 0.96	-0.09 ± 0.26, t = -0.34, p = 0.74
	3	37.10 ± 2.40, t = 15.46, p < 0.001	2.18 ± 1.82, t = 1.19, p = 0.24	0.19 ± 1.83, t = 0.10, p = 0.92	-2.63 ± 1.80,t = -1.46, p = 0.15
	4	48.81 ± 0.63, t = 6.93, p < 0.001	0.51 ± 0.78, t = 0.65, p = 0.52	-0.63 ± 0.73, t = -0.88, p = 0.39	-0.62 ± 0.72, t = -0.87, p = 0.39
	4b	50.73 ± 1.01, t = 50.21, p < 0.001	1.01 ± 0.96, t = 1.05, p = 0.30	-0.20 ± 0.92, t = -0.22, p = 0.83	-0.30 ± 0.92, t = -0.33, p = 0.75

Table 4: Standardized estimates ± standard errors for the three top ranked models by the AIC_C model selection from the nonlinear curve fitting in the analysis of (A): reproductive phenology with the parameter b (inversely related to the phenological phase at day 0) as response variable, (B): reproductive phenology with the parameter c (rate of reproductive phenological development) as response variable, (C): vegetative phenology with the parameter b (inversely related to the phenological phase at day 0) as response variable, (D): vegetative phenology with the parameter c (rate of reproductive phenological development) as response variable. Estimates are relative to control, where Intercept = control treatment, I = icing treatment, IW = combined icing and warming treatment, W = warming treatment and Natural Ice = thickness of natural occurring ice. w_i = AIC_C weight. The interaction species-treatment was also included as explanatory variable in a global model, however not present among the top ranked models and hence not included in this table.

		Explanatory variables				**Model selection criteria**		
	Rank	**Intercept**	**Species**	**Treatment**	**Natural Ice**	**AIC_C**	**ΔAIC_C**	**w_i**
A	**1**	C: -0.05 ± 0.14		I: 0.19 ± 0.17 IW: -0.47 ± 0.16 W: -0.70 ± 0.14	0.10 ± 0.05	334.63	0	0.75
	2	C: 0.03 ± 0.13		I: 0.17 ± 0.17 IW: -0.47 ± 0.16 W: -0.66 ± 0.15		336.84	2.21	0.25
	3	C: *A. borealis*: -0.09 ± 0.19	*S. polaris* (female): -0.06 ± 0.21 *S. polaris* (male): -0.01 ± 0.18 *B. vivipara*: 0.14 ± 0.19 *L. confusa*: 0.15 ± 0.23 *P. arctica*: 0.07 ± 0.22	I: 0.20 ± 0.16 IW: -0.49 ± 0.15 W: -0.72 ± 0.14	0.10 ± 0.05	344.26	9.64	0.01
B	**1**	-0.26 ± 0.18			0.13 ± 0.07	415.33	0	0.43
	2	-0.14 ± 0.16				415.71	1.46	0.21
	3	-0.23 ± 0.21		I: -0.28 ± 0.20 IW: 0.16 ± 0.20 W: 0.09 ± 0.20	0.11 ± 0.07	416.92	1.59	0.20
C	**1**	-0.06 ± 0.19				195.78	0	0.56
	2	-0.14 ± 0.21			0.09 ± 0.12	197.81	2.03	0.20
	3	0.25 ± 0.30		I: -0.22 ± 0.40		199.87	4.09	0.07

				IW: -0.20 ± 0.39 W: -0.85 ± 0.40				
D	**1**	-0.12 ± 0.49				189.34	0	0.43
	2	-0.19 ± 0.51			0.08 ± 0.09	190.93	1.59	0.20
	3	0.27 ± 0.44		I: -0.65 ± 0.26 IW: -0.52 ± 0.26 W: -0.45 ± 0.26		192.38	3.04	0.10

Table 5: Overview of samples sizes. Mean number of sub-squares of the vegetation frame (sub-divided in 16 sub-squares, see Figure 4), used for phenology registrations, a species was present in, through the field season. Each row represents a specific plot (in each of the three blocks, A, B and C) in a specific treatment. C = control, I = icing, IW = icing and warming and W = warming.

			S. polaris (female)		***S. polaris (male)***		***B. vivipara***		***P. arctica***		***A. borealis***		***L. confusa***		***S. polaris (vegetative)***		***B. vivipara (vegetative)***	
Treatment	**Block**	**Plot**	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
C	A	3	10.67	2.69	16.00	0.00	0.00	0.00	6.08	1.50	0.18	0.37	1.00	0.49	16.00	0.00	8.25	1.16
		5	12.58	0.95	12.08	1.61	3.33	2.92	1.25	0.92	1.82	0.75	0.00	0.00	16.00	0.00	15.92	0.28
		7	8.00	0.82	8.17	0.69	3.00	1.63	5.33	0.85	0.00	0.00	0.00	0.00	16.00	0.00	16.00	0.00
	B	3	6.25	0.43	3.75	0.60	8.33	1.49	1.42	1.55	3.36	1.98	0.00	0.00	13.50	0.96	14.42	0.76
		7	6.08	2.53	16.00	0.00	3.42	1.44	10.33	2.49	0.00	0.00	1.09	0.41	16.00	0.00	15.08	0.76
		8	11.08	0.28	10.00	0.00	4.33	2.49	0.17	0.55	0.91	0.80	0.00	0.00	16.00	0.00	15.92	0.28
	C	1	14.33	0.47	4.00	0.00	7.67	3.12	2.67	1.49	2.00	1.14	5.82	1.65	16.00	0.00	15.92	0.28
		4	0.92	0.28	13.17	0.37	7.00	2.71	1.25	0.92	1.64	0.96	0.00	0.00	16.00	0.00	15.17	0.37
		9	5.67	0.94	1.00	0.00	10.67	2.25	0.00	0.00	2.09	1.61	1.00	0.49	16.00	0.00	15.00	0.41
I	A	4	1.83	1.14	14.92	0.28	3.33	2.21	0.00	0.00	0.00	0.00	0.00	0.00	16.00	0.00	15.92	0.28
		10	15.00	0.00	4.33	0.85	3.75	2.62	1.83	1.07	1.45	0.75	0.00	0.00	16.00	0.00	13.33	1.03
		12	9.92	0.86	13.25	0.43	5.50	3.50	2.83	1.72	1.55	1.19	0.00	0.00	15.92	0.28	16.00	0.00
	B	4	4.00	1.41	7.58	0.76	5.08	2.87	1.25	0.72	0.09	0.28	0.91	0.37	16.00	0.00	15.83	0.55
		6	5.75	0.83	15.00	0.00	1.17	0.90	0.00	0.00	0.73	0.62	0.00	0.00	16.00	0.00	15.17	0.37
		9	2.42	0.64	14.00	0.58	0.25	0.60	0.00	0.00	0.00	0.00	0.00	0.00	16.00	0.00	15.92	0.28
	C	5	10.33	0.47	6.25	0.83	6.58	1.98	0.00	0.00	0.82	0.43	1.64	0.76	16.00	0.00	1.42	3.06
		6	6.17	3.21	4.50	4.33	0.67	0.75	0.00	0.00	0.00	0.00	0.00	0.00	16.00	0.00	3.17	1.07
		12	11.00	0.91	11.67	1.03	7.42	2.06	1.08	0.86	0.09	0.28	0.09	0.28	16.00	0.00	12.33	2.17
IW	A	2	14.17	1.21	11.83	1.52	3.92	1.32	0.75	0.43	0.91	0.69	0.00	0.00	16.00	0.00	12.83	0.69
		6	2.00	0.41	4.25	1.16	14.67	1.97	0.42	0.49	0.00	0.00	0.00	0.00	16.00	0.00	16.00	0.00

		8	13.75	0.72	10.92	0.49	7.00	1.58	3.33	1.25	0.09	0.28	0.00	0.00	16.00	0.00	15.92	0.28
	B	5	7.08	1.04	5.33	2.01	5.83	2.34	0.33	0.47	0.64	0.64	0.00	0.00	15.92	0.28	15.08	0.28
		10	13.58	2.10	5.08	0.28	7.92	2.96	0.00	0.00	0.00	0.00	0.00	0.00	16.00	0.00	15.00	0.82
		11	8.00	1.35	3.25	0.60	2.58	1.32	0.00	0.00	0.00	0.00	0.00	0.00	16.00	0.00	15.92	0.28
	C	7	1.83	0.37	1.17	0.37	10.08	2.63	6.08	2.78	1.45	0.75	3.55	1.23	16.00	0.00	15.75	0.60
		8	0.08	0.28	7.50	0.96	3.25	0.83	4.33	1.37	2.00	1.07	1.27	0.69	16.00	0.28	7.08	0.28
		10	8.75	0.60	3.08	0.86	6.92	1.85	0.67	0.75	0.18	0.37	0.09	0.28	15.75	0.60	12.00	0.71
W	A	1	11.33	1.25	1.92	0.28	6.50	1.44	9.67	1.43	0.00	0.00	0.00	0.00	16.00	0.00	14.67	0.47
		9	12.83	0.55	5.00	0.41	8.42	2.06	15.00	1.15	3.36	2.06	1.36	0.60	16.00	0.00	15.75	0.60
		11	2.58	0.64	3.42	0.76	12.83	0.80	4.58	1.50	3.91	2.29	1.00	0.28	16.00	0.00	14.83	0.55
	B	1	13.83	0.55	5.67	0.62	5.67	1.84	1.08	0.49	0.09	0.28	0.00	0.00	16.00	0.00	14.92	0.28
		2	2.50	0.96	13.08	0.28	5.00	2.16	0.17	0.37	1.09	0.58	0.09	0.28	16.00	0.00	15.83	0.37
		12	5.75	1.29	4.50	0.87	7.67	2.05	0.00	0.00	0.00	0.00	0.00	0.00	16.00	0.00	15.92	0.28
	C	2	0.00	0.00	0.00	0.00	11.50	2.47	5.67	2.17	3.09	1.91	8.55	2.44	0.00	0.00	15.33	1.49
		3	3.58	0.49	8.92	0.95	4.50	1.26	0.00	0.00	2.00	1.40	8.55	1.44	15.92	0.28	15.67	0.85
		11	0.00	0.00	0.00	0.00	12.58	0.76	0.00	0.00	7.45	3.93	6.45	2.12	0.00	0.00	15.67	0.75
Total			**7.32**	**4.73**	**6.06**	**3.52**	**2.43**	**3.44**	**1.19**	**1.54**	**1.18**	**2.33**	**6.06**	**3.52**	**15.03**	**3.67**	**14.03**	**3.48**