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Effects of Experimental Icing and Summer Warming on the Polar Willow *Salix polaris* on Svalbard

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Abstract

The effects of climate change are particularly strong in the Arctic, where temperatures are increasing rapidly. While a clear trend of a more productive and greener Arctic in response to summer warming has been confirmed by several studies, recent assessments suggest that the Arctic is browning. In some regions, more frequent extreme winter rain-on-snow (ROS) events, resulting in ground ice encapsulating the vegetation are predicted with climate warming. In this study from high Arctic Svalbard (78°N), I investigate how the dwarf shrub *Salix polaris*, an important food source for herbivores, is affected by a warmer climate in a full-factorial field experiment. Warmer summer temperatures were induced using open top chambers, while heavy winter ROS was simulated by experimentally applying 'ROS' and thereby encasing the vegetation in about 13 cm solid ice. No impacts of experimental icing on *S. polaris* annual stem length, leaf biomass or flower production were found, possibly reflecting the robustness of the shrub. However, *S. polaris* responded to increased summer temperatures by decreasing its flower production and producing shorter annual stem length. The leaves also got heavier per surface area (reduced specific leaf area), but not larger (area or length), due to warming. Surprisingly, the total productivity of the plant community was found to be enhanced by winter icing, and not to be affected by summer warming, indicated by their effects on peak season Normalised Difference Vegetation Index. My results on *S. polaris* indicate that summer warming and winter icing may pull in different directions, but their relative importance is still unknown.

Abstract in Norwegian

Effektene av klimaendringer er spesielt store i Arktis, hvor temperaturene øker raskt. Samtidig som en tydelig trend mot et mer grønt og produktivt Arktis i respons til sommervarming har blitt bekreftet av flere studier, viser nyere undersøkelser at Arktis blir brunere. I enkelte områder har det blitt predikert mer hyppige tilfeller av ekstremt vinterregn (ROS) som følge av klimaendringer, hvilket resulterer i dannelsen av bakkeis som dekker vegetasjonen. Dette studiet fra høyarktiske Svalbard (78°N) undersøker hvordan dvergbusken *Salix polaris*, en viktig matkilde for planteetere, påvirkes av de forventede klimaendringene i et fullt faktorielt felteksperiment. Varmere sommertemperaturer ble indusert ved å bruke 'open top chambers' (drivhus uten tak), mens en kraftig hendelse av ROS ble simulert ved å eksperimentelt påføre 'ROS' slik at vegetasjonen ble innkapslet i omtrent 13 cm tykk is. Det ble ikke funnet noen effekt av eksperimentell ising på *S. polaris* årlig stammelengde, biomasse eller blomsterproduksjon, noe som antyder robuste egenskaper hos planten. Når det gjelder økt sommertemperatur, responderte *S. polaris* ved å redusere årlig stammelengde og minke blomsterproduksjonen. Bladene ble tyngre per overflateareal (redusert spesifikt bladareal), men ikke større (areal eller lengde). Noe overraskende, økte plantesamfunnets totale produktivitet med vinter-ising, men ble ikke påvirket av sommervarming, basert på deres effekt på 'Normalised Difference Vegetation Index' i høysesongen. Mine resultater på *S. polaris* indikerer at sommervarming og vinterising kan trekke i ulike retninger, men deres relative betydning er fremdeles ikke kjent.

Contents

1

Introduction

With increasing global temperatures, a wide range of species and ecosystems are affected (Walther et al., 2002; Parmesan, 2006; Parmesan and Yohe, 2003; IPCC, 2014). The effects of climate change are particularly strong in the Arctic, where temperatures are rising rapidly (AMAP, 2011; IPCC, 2014). Experiments have shown substantial impacts of longer and warmer growing seasons on Arctic tundra vegetation (Hudson et al., 2011). A positive effect of warming has been found on the growth of several plant species, with a drastic increase in above-ground productivity in response to even minor temperature increases (van der Wal and Stien, 2014). While a clear trend of a more productive and greener Arctic in response to summer warming has been confirmed by several studies (Walker et al., 2012; Raynolds et al., 2008; Xu et al., 2013), NOAA (Epstein et al., 2015) recently suggested that the Arctic is browning, by reporting decreased greenness. Furthermore, the response to warming may differ between species and growth forms (Preece et al., 2012; Elmendorf et al., 2012; Arft et al., 1999). Thus, this may lead to decreased species diversity and evenness in the long-term (Walker et al., 2006; Chapin et al., 1995). In parts of the Arctic tundra, changes in the vegetation structure are expected with an increase in shrub cover in response to climate warming (Walker et al., 2006; Callaghan et al., 2011; Chapin et al., 1995).

The increase in shrub cover is expected to be most extensive in Arctic tundra areas dominated by tall shrubs, experiencing warm ambient temperatures and high soil moisture, whereas cold tundra vegetation could primarily experience an increase in graminoids (Elmendorf et al., 2012). In cold tundra regions, the tallest growth forms tend to be herbaceous (often graminoids), which easily overtop dwarf shrubs. Accordingly, Elmendorf et al. (2012) suggest that species capable of vertical growth are favoured by warming in these environments. Prostrate dwarf shrubs such as the focal polar willow (*Salix polaris*), may hence be outcompeted by graminoids in a warmer high Arctic climate. The annual above-ground biomass of *S. polaris* has been shown to follow the annual fluctuations in June-July temperature (van der Wal and Stien, 2014). Accordingly, synchrony in *S. polaris* growth over long distances across Svalbard is partly due to summer temperature (Sandal, 2017). Synchronous growth alterations in *S. polaris* across Svalbard can thus negatively affect the wild reindeer, which is dependent on the shrub as a food source throughout most of the year (Bjørkvoll et al., 2009).

Responses to summer warming on the species level are often easily documented through experimental warming. However, the impacts of winter climatic change on species are far from understood (Cooper, 2014). Future warming in the high Arctic is expected to be stronger during winter than summer (AMAP, 2011). Several studies (Rennert et al., 2009; Hansen et al., 2014) have predicted that a consequence of Arctic warming could be an increased frequency of rain-on-snow (ROS) events. As periods with abnormally warm temperatures and heavy ROS events on frozen ground occur more frequently during winter, formations of ice layers will encapsulate the plants, and consequently affect the herbivore community (Hansen et al., 2013; Hansen et al., 2014). Winter rain melts the snow which freezes to solid ice (Putkonen and Roe, 2003), and the ground ice layer, with a thickness up to 20 cm, could cover most of the short-growing vegetation on the high Arctic tundra (Hansen et al., 2014).

The consequences of ROS events on tundra plants are widely unknown. However, a study from high Arctic Svalbard (Milner et al., 2016), recently showed that flowering frequency and shoot survival in the shrub *Cassiope tetragona* were severely negatively affected by experimental icing. The plants with more flowers invested less in shoot growth, and undamaged shoots showed higher growth with icing. This shrub is not eaten by herbivores, and it is hence not known how forage plant species are affected by icing. Although previous studies have shown that resident herbivores are strongly influenced by ROS events and ground icing through the accessibility to forage in winter (Hansen et al., 2013), we do not know much about how the food resources such as *S. polaris* are affected. Studies on dominant dwarf shrubs from the sub-Arctic browsed by herbivores does however, indicate that some dwarf shrubs respond to experimental icing by decreased flowering and increased shoot mortality (Preece et al., 2012; Preece and Phoenix, 2014).

In a time-series study of retrospective 'tree-ring' growth in *S. polaris*, summer temperatures were found to modulate annual growth (Buchwal et al., 2013). However, a recent study (Sandal, 2017) indicates that extreme winters, do have a negative effect on this species' annual growth that may potentially modify the effects of summer warming. Woody plants of the high Arctic are expected to be resilient to cold temperatures by winter hardening (Callaghan et al., 2005), and winter temperature is hence not a limiting factor. However, with ice encasement plants get exposed to low oxygen conditions which can cause damage as a result of cellular dehydration and anoxia injuries (Preece and Phoenix, 2014). Still, Arctic plants may be more resilient to anoxia than plants of the same species from lower latitudes (Crawford et al., 1994).

Given the expected increase in both summer temperature, warm spells (Moore, 2016) and rain events in winter (Hansen et al., 2014), understanding how the tundra species of high ecosystem importance like *S. polaris* respond to winter icing and summer warming is fundamental for our understanding of future ecosystem-level changes. Due to the importance of vegetation structure and productivity for both overwintering and migratory herbivores, this is essential.

The overall aim of this study is to shed some light on the effects of warmer summer temperatures and winter ground icing, and their possible interaction effects on *S. polaris*. In addition, I examine and discuss the overall community response, in terms of Normalised Difference Vegetation Index (NDVI) and vegetation structure, in relation to the results on *S. polaris*. I will investigate (1) growth, i.e. annual stem length, (2) leaf biomass, i.e. specific leaf area (SLA) and weight, (3) flower production, i.e. number of catkins, (4) the abundance of *S. polaris* as number of hits in Point Intercept Method (PIM)*,* and (5) overall species abundance/cover, as number of hits in PIM.

Warming can be expected to have positive effects on growth, biomass and reproduction in *S. polaris* (Dormann et al., 2004; Robinson et al., 1998; Buchwal et al., 2013; Sandal, 2017). However, one might expect the potential positive effect of experimental warming to be altered by competing species such as taller growing graminoids (Elmendorf et al., 2012; Dormann et al., 2004). *S. polaris* is expected to be rather resilient to cold temperatures (Callaghan et al., 2005), but ice encapsulation of the vegetation following simulated ROS-events, may be expected to cause negative responses in shrubs, with possible trade-offs between vital rates (Milner et al., 2016). By investigating the response of *S. polaris* to experimental winter icing and summer warming, this study will therefore contribute to our understanding of the net effects of climate warming as well as the indirect implications for higher trophic levels.

2

Methods

2.1 Study Area and Target Species

This study was conducted in Adventdalen (Spitsbergen) close to Longyearbyen, Svalbard (78° 13`N, 15° 38`E). The study area and experimental design have been described in detail by Hovdal (2017), but necessary details are given here. Mean annual temperatures range from -11.9°C in winter to 4.7°C in summer (mean temperatures from 1960 – 2016), and annual precipitation is low (mean = 197 mm, SD = 47 mm) (Norwegian Meteorological Institute). The experimental sites in Adventdalen were in an overall flat and mesic area in the central part of the valley (Figure 1b). Vegetation is dominated by the dwarf shrub *Salix polaris,* the mosses *Sanionia uncinata, Tomentypnum nitens* and *Polytrichum spp.*, the herb *Bistorta vivipara* and the graminoids *Alopecurus borealis, Poa arctica* and *Luzula confusa.* Throughout the year, the area is heavily grazed by wild Svalbard reindeer, and during spring and summer additionally by barnacle- and pink-footed geese.

The focal species of this study is the polar willow (*S. polaris* Walenberg, Salicaceae) (Figure 1a). *S. polaris* is a low, prostrate dwarf shrub, usually less than 2 cm in height (Lid et al., 2005; Rønning, 1996). The species has a relatively slow colonisation rate, and its competitive ability is low (Dormann et al., 2004). However, once established, it persists in numerous communities due to its high stress tolerance (Nakatsubo et al., 2010). It is widely distributed across high Arctic tundra communities, where it is commonly the dominant plant species (Bliss and Matveyeva, 1992). It shows a broad range of soil moisture tolerances, from wetlands to polar deserts (Callaghan et al., 2005). Annual stem length is 5-10 mm, and the leaves are about 1 cm in diameter, thick, oval and dark green. The leaves senescence early by changing colour (end of August). *S. polaris* is dioecious and reproduces both sexually and vegetatively by rhizomes (Rønning, 1996). Both anemophily (wind-pollination) and entomophily (insect-pollination) likely occur, but their relative importance is unknown.

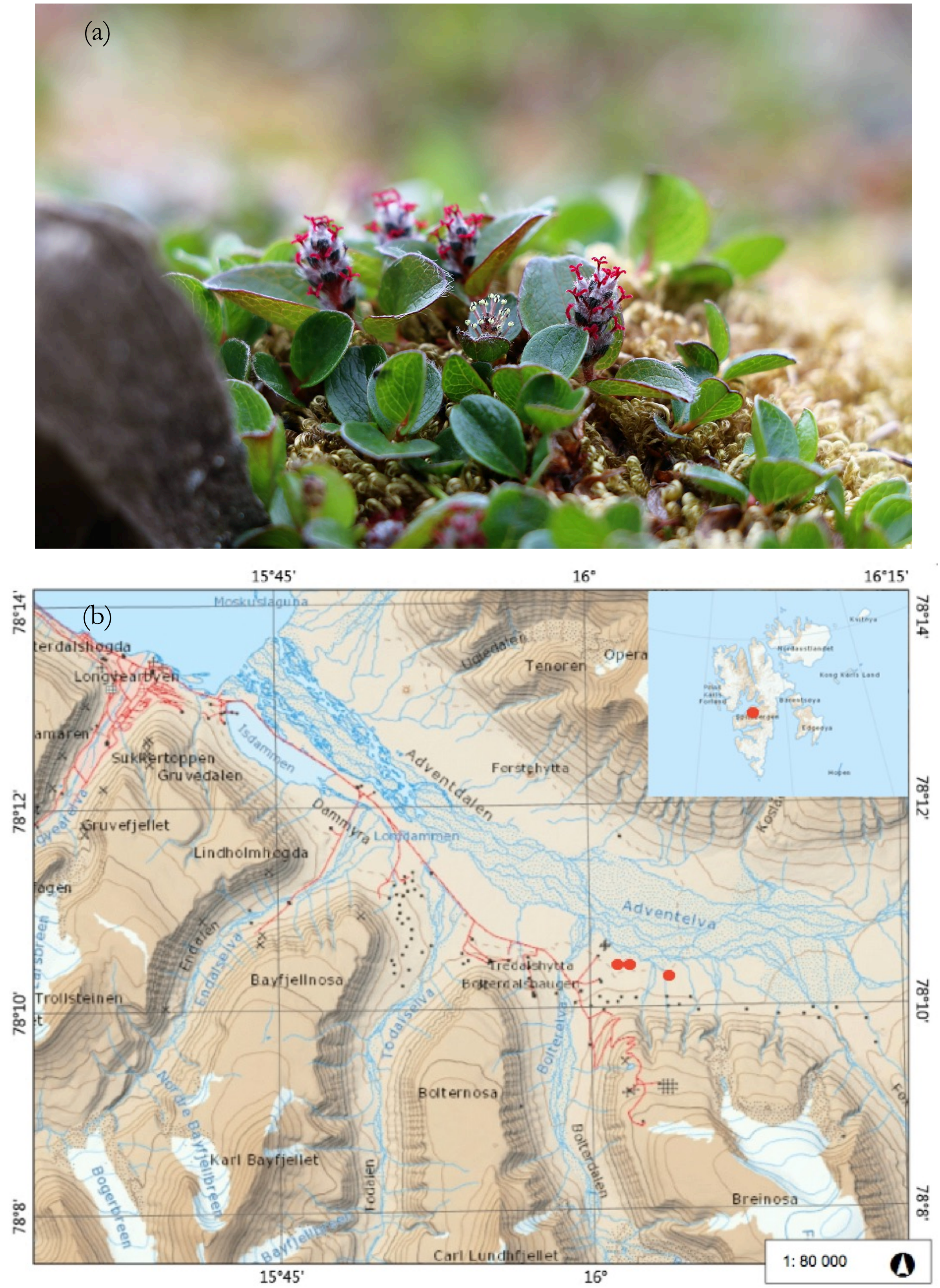

Figure 1. (a) *Salix polaris* with male (white) and female (red) catkins. Photo: Katrín Björnsdóttir. (b) Map of the study blocks (marked with red points) in Adventdalen, Svalbard. Longitude-Latitude coordinates are shown at the map border and map scale in the bottom-right corner. © Norwegian Polar Institute.

2.2 Field Experimental Design

The experiment was a full factorial, generalised and randomised block design and was run in three mesic sites (referred to as blocks) in Adventdalen. The blocks (approximately 20 x 20 m) had relatively homogeneous moss tundra vegetation and were selected at the end of summer 2015. The three sites were between 150 m and 780 m apart from each other, and between them, other vegetation communities were present. Each block consisted of 12 plots (12 plots x 3 blocks = 36 plots in total). Plots (50 x 50 cm) were selected to have a relatively homogeneous plant community composition and were at least 2 m apart from each other.

The 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 different treatment combinations; C = control plots (i.e. no icing, ambient temperatures), I = plots treated with experimental icing and ambient temperatures, W = plots with no icing, treated with experimental warming and IW = plots treated with experimental icing and warming. Each treatment combination was replicated three times in each block and was assigned to the plots following a randomisation process (Figure 2). Control plots had ambient temperatures and were not treated with icing.

The icing treatment was performed on 4th – 5th of February 2016 to simulate the icing effect occurring after ROS events on Svalbard. In each of 3 blocks x 6 plots = 18 plots, the snow was removed from the plot area. Snow depth and the naturally occurring ice was measured, also in control plots (see details in Hovdal, 2017). A 60 x 60 cm wooden frame (13 cm high) was placed on the ground and, in cold weather, gradually filled with cold water (mixed with snow). The ice encasement occurred gradually over two days until the wooden frames were filled with solid ground-ice, to mimic the natural build-up of ground-ice following heavy ROS events (see Milner et al. 2016). The wooden frames were removed when the ice and snow melted (May 20th).

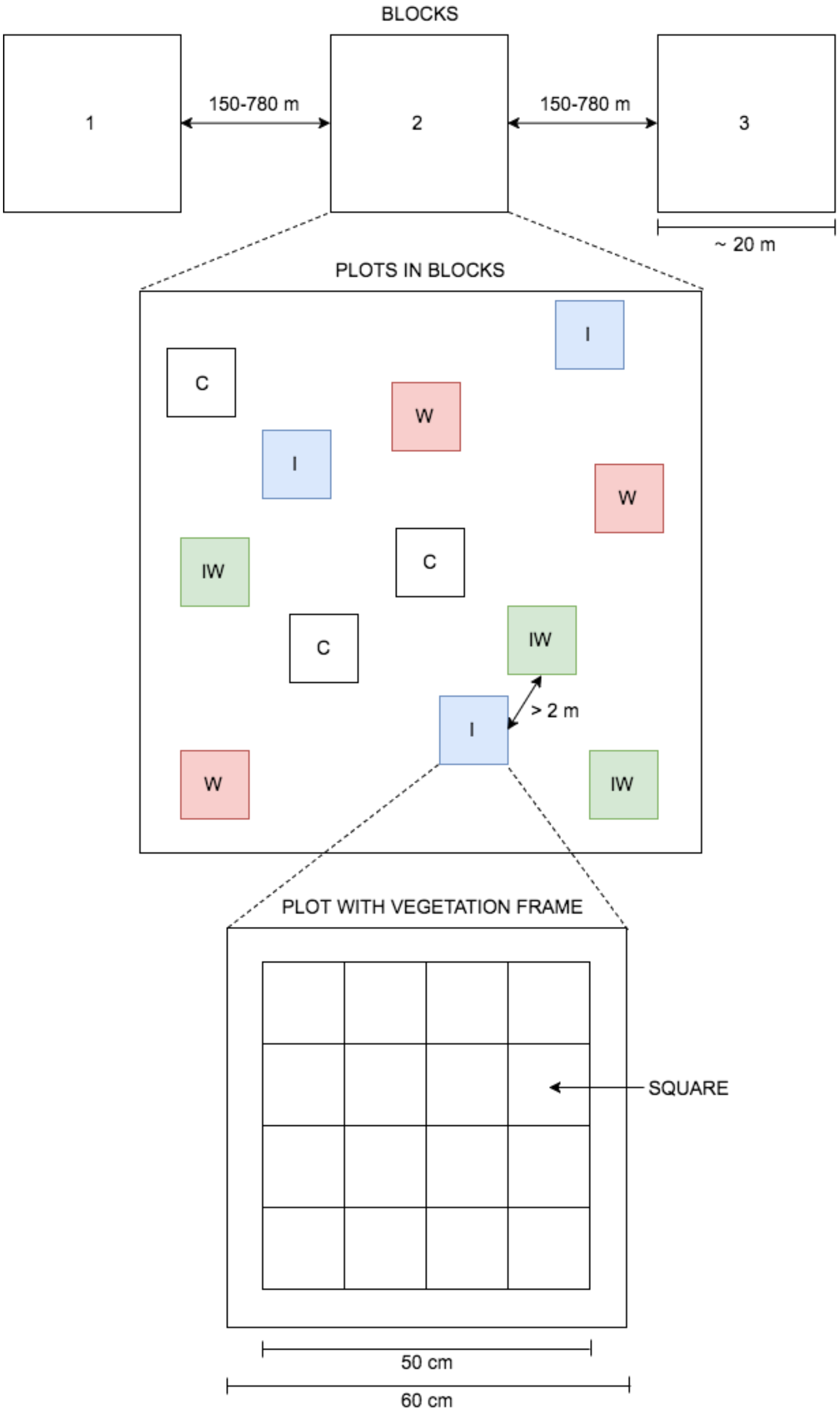

Figure 2. Illustration of the experimental design with 12 plots in each of the three blocks (adapted from Hovdal, 2017). Blocks (approximately 20 x 20 m) were between 150 m and 780 m apart from each other. C = control plots (i.e. no icing, ambient temperatures), I = plots treated with experimental icing and ambient temperatures, W = plots with no icing, treated with experimental warming, IW = plots treated with experimental icing and warming. Icing plots were treated within an area of 60 x 60 cm. The warming plots were treated in the area spanned by the OTCs, i.e. a hexagon with 100 cm in base diameter (38.5 cm tall). To account for edge effects, the vegetation frame used for measurements was 50 x 50 cm with 16 sub-squares (referred to as squares).

Open top chambers (OTCs) were placed May 23rd in 18 of the plots (3 W + 3 IW = 6 plots in each block) after the snow had melted to simulate warmer summer temperatures. OTCs were originally developed for the International Tundra Experiment (ITEX) (Henry and Molau, 1997). They are now widely used in experimental studies of climate warming effects in plants, both in Arctic and alpine regions, because of their significant temperature altering without unwanted ecological effects (Marion et al., 1997; Hollister and Webber, 2000).

Exclusion of herbivores was performed from the 29th of May. OTCs were covered with metal nets. In the other plots (I, C), a metal net was wrapped around a thin wooden frame with approximate size 60 x 60 x 50 cm (Figure 3). The OTCs and cages were secured with tent plugs.

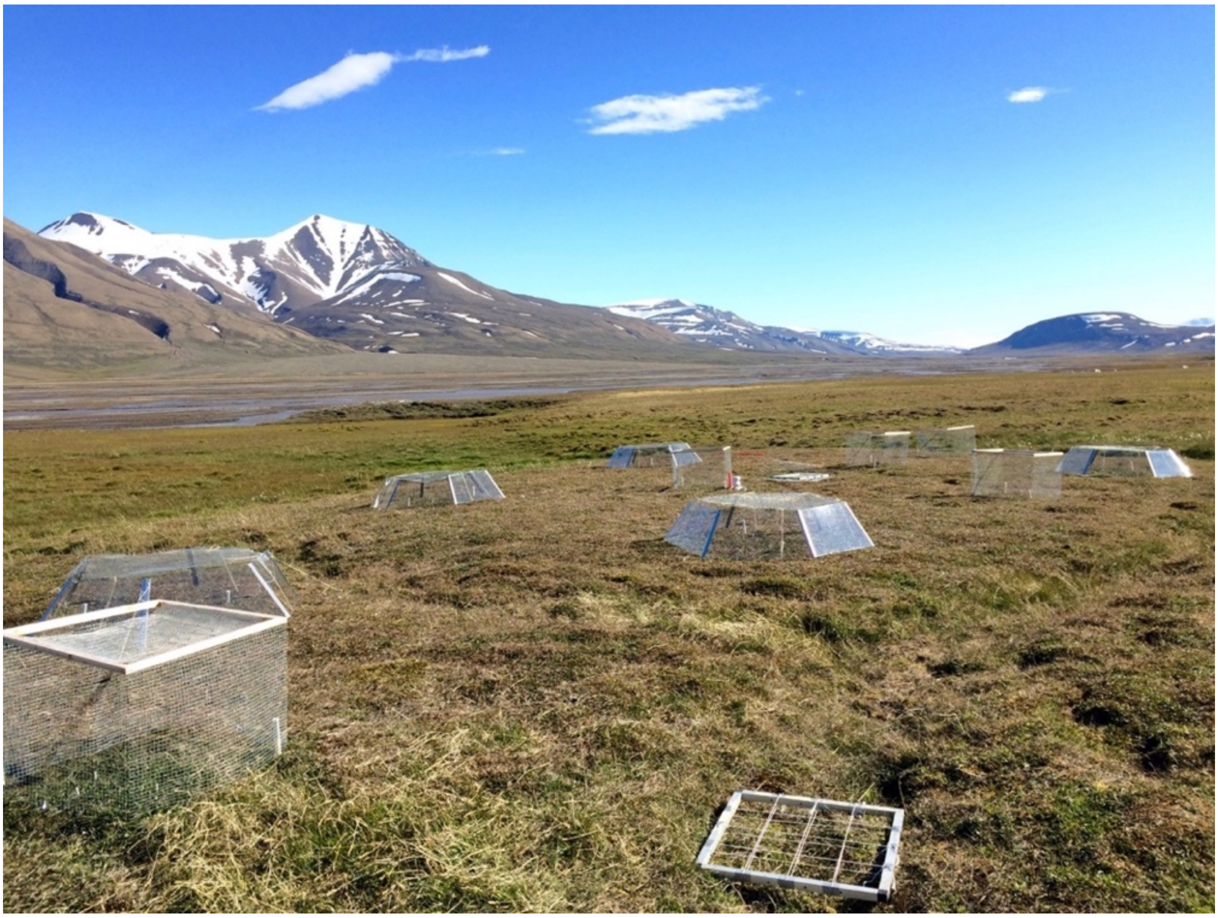

Figure 3. One of the three experimental sites (blocks) in Adventdalen during summer 2016.

2.3 Measurements

Given that ground ice was occurring naturally in some of the plots, the mean natural ice thickness was measured in each plot (January 2016). During peak season (August 5th, 2016), all leaves from seven above-ground branches (top shoots) of *S. polaris* were randomly sampled from each plot. The top shoots were chosen by using a vegetation frame (50 x 50 cm, Figure 2) with 16 evenly divided smaller squares made of a double string on top of the plots. The points created by the crossing strings (9 in total) were used as a reference to which shoots to pick. Starting at the first cross, the closest shoot was picked using scissors, and repeated in the next crosses until seven shoots were picked (*S. polaris* was absent in one of the plots). From each plot, the stems were put in a separate plastic bag and the leaves in paper tea bags. By using this method, it was possible to link the leaves and stems to specific plots, but unfortunately not leaves to their stem.

Immediately after the sampling, the tea bags with leaves were put inside a larger plastic bag with a zip-lock in a fridge. To ensure that moisture was kept, a moist paper towel was placed inside the plastic bag, but not in contact with the samples, to avoid freezing of the leaves. The stems were put in another plastic bag following the same procedure. The samples were kept in the fridge for two-three days. The stems were scanned with a fully automated stereo microscope (Leica M205), using the imaging software Leica Application Suite (LAS 4.3). Image J was used to measure the length of the 2016 increment, using the bud scars as a reference.

To measure leaf characteristics, the petioles were removed, and the leaves were placed on a scanner with millimetre paper so that the leaves were slightly pressed in the process. The scanned images were analysed with Image J, to determine leaf length and one-sided leaf area. After the scanning process, the leaves were dried to constant weight (48 - 96 hours) at 60°C and placed in a desiccator for cooling before weighing them individually at room temperature (using a Mettler-Toledo XS204 DeltaRange scale). Following Perez-Harguindeguy et al. (2013) SLA is the ratio between one-sided leaf area (unit = mm^2) by its corresponding oven-dry mass (unit = mg).

Flowering frequency was measured by counting the inflorescences (catkins) of *S. polaris* once during the growing season (July 13th – 15th, 2016). Female and male catkins were counted in each square (10 x 10 cm) of the vegetation frame (50 x 50 cm, 16 squares) placed in the plot area.

At the peak of the growing season (August 2^{nd} - 4^{th}, 2016), PIM (Levy and Madden, 1933; Goodall, 1952) was performed to measure the abundance of *S. polaris* and to surrogate its biomass (Jonasson, 1988) in each plot. For this method, a vegetation frame (50 x 50 cm, 25 squares) with a double layer of strings was used. A pin was dropped vertically at each cross created by the strings, and all hits of vascular plants through the vegetation canopy were noted as well as bryophytes, lichens and dead plant material in the sward (the final hit). The procedure was repeated in all crosses, and hits were identified at the species level if possible, otherwise at the genus or family level.

As an indirect measure of productivity of the general plant community, a Skye SpectroSense2+ hand-held meter was used to measure the NDVI of the plots (Sellers, 1985; Tucker and Sellers, 1986; Prince, 1991). The sensors were placed in the centre of the plots making sure the meter did not cast any shade, with a radius of 25 cm so that the whole plot (50 x 50 cm) was covered. Mean soil moisture was measured three times during the season with a moisture meter (HH2 Moisture Meter with Delta-T soil moisture sensor).

To get an estimate of the OTC-effect (warming treatment) on temperature, soil surface temperature was measured through the summer in all warming- and control plots (W: mean = 7.3 °C, SD = 1.4 °C, C: mean = 6.3 °C, SD = 1.5 °C). Additionally, air temperatures were measured inside one of the OTCs and in one control plot, at 10 cm above the surface by HOBO-loggers (W: mean temperature = 9.4 °C, SD = 2.9 °C, C: mean temperature = 8.5 °C, SD = 2.3 °C).

2.4 Statistical Analysis

2.4.1 Univariate Analysis

To test for treatment effects of experimental icing and warming on *S. polaris* traits*,* I used linear mixed effect models, with the 'lme4' package in R (Bates et al., 2016), to take the hierarchical structure of the data into account. The analysis was done at the plot level for all traits except for the number of flowers (catkins), where it was done at the frame-square level (as 16 per plot). In all models with more than one measurement per plot, the random factor (random intercept) was defined as plot nested within block (otherwise block was the only random factor). The models for the number of catkins and *S. polaris* abundance assumed a Poisson distribution for the response variable. Thus, I used generalised linear mixed effect models (glmer) with a log link. I tested for overdispersion in the glmer models and found indications that the flower model was slightly overdispersed obtained by the function 'dispersion_glmer' in the 'blemco' package (Nievergelt et al., 2015). Therefore, I used a negative binomial distribution, which accounts for overdispersion. The abundance model did not appear to be overdispersed. For all other response variables (i.e. annual stem length, leaf weight, leaf length, leaf area, leaf weight given area, SLA and NDVI) I used linear mixed effect models.

For model selection I used the Akaike Information Criterion corrected for small-sample bias (AICc) (Burnham and Anderson, 2001). When comparing models, it is common to measure how much more parsimonious (i.e. explains the most variance using the least parameters) the best model is compared to other models. A model with ΔAIC_c of 2 or less is considered to more substantially support the data, relative to other candidate models (Burnham and Anderson, 2001). However, I chose to show parameter estimates of the top-ranked model only (see Appendix).

Note that the main effects of experimental treatments (warming and icing) were included in all subsets of the global models. Models were fitted using maximum likelihood (ML), and the following predictor variables were included in all global models: icing (0,1), warming (0,1), and the interaction, natural ice thickness, mean soil moisture (average from the whole season) and *S. polaris* abundance (not in the model for abundance). Icing and warming were included in all models, regardless of their significance, to show their effect sizes. The other explanatory variables were included as nuisance parameters to account for their effect, since I was mainly interested in the effects of warming and icing. Since the predictor variables were not measured on the same scale, they were all (except icing and warming) standardised prior to model fitting. *S. polaris* abundance was included in the models to account for effects of plot-specific abundance. Other covariates that

I considered might influence certain response variables were additionally included (i.e. annual stem length in leaf characteristic models to account for plot-specific stem length, and mean NDVI in the abundance model to account for the plot-specific total productivity). Natural ice thickness and soil moisture were not significantly correlated ($r = 0.07$, $n = 36$, $p = 0.67$), and could both be included in the global models to correct for plot-specific, naturally occurring environmental conditions. Top models were fitted with REML after model selection to obtain parameter estimates (Bates, 2014).

2.4.2 Multivariate Analysis

Leps and Smilauer (2003) recommend using PCA when the gradient length is short (i.e. low beta diversity). However, PCA (principal component analysis) has been found to always produce unwanted edge effects (Økland, 1990). Additionally, others (Minchin, 1987) have found PCA to generate a poorer result compared to DCA and NMDS by ordination of species-location data. I used parallel ordination following recommendations from Økland (1996), as ordination methods may distort the true gradient structure of the data. Hence, two principally different ordination methods, DCA (detrended correspondence analysis) (Hill and Gauch, 1980) and GNMDS (global non-metric multidimensional scaling) (Minchin, 1987), were used, to assess possible treatment effects on species composition.

Dead material was for simplicity, excluded from the multivariate analysis. DCA and GNMDS were performed by using the 'vegan' package in R (Oksanen et al., 2012), to analyse the community structure. DCA was performed by the 'decorana' function with standard options: detrending by segments and non-linear rescaling of axes in standard deviation-units. GNMDS ordination was obtained by the functions 'vegdist', 'isomapdist', 'monoMDS' and 'postMDS', and was performed with the following options: distance measure = Bray-Curtis distance, dimensions = 2, initial configuration = 100, maximum iterations = 2000 and convergence ratio for stress = 1e-07. The GNMDS axes were subject to varimax rotation and were rescaled linearly into half-change units. Procrustes analysis (permutations = 999) was done to compare the GNMDS solutions with the lowest and second lowest stress. The similarity between pairs of DCA and GNMDS ordination axes were evaluated by calculating Kendall's nonparametric correlation τ (pair-wise) between sampling unit scores (Kendall, 1938).

All statistical analyses were carried out in R (version 3.3.1) (R Core Development Team, 2017).

3

Results

3.1 *Salix polaris* Traits

Warming and icing were kept in all models, even if they were not present in the best model after model selection (i.e. forced into the models) so that any trends in their effect could be observed. The top model for annual stem length did not include any of the proposed covariates. However, warming and icing were included to assess their effect. Stem length was reduced with experimental warming ($P < 0.05$, Figure 4b, Table 1). The experimental icing did not have a significant effect on stem length ($P = 0.22$, Figure 4a, Table 1). The top-ranked model for leaf weight, length, area and SLA, included warming, icing and stem length. Neither of these leaf traits were affected by experimental icing (SLA: $P = 0.77$, Figure 4e, weight: $P = 0.62$: Figure 4c, length: $P = 0.72$, area: $P = 0.54$, Table 1). However, warming had a negative effect on SLA ($P < 0.05$, Figure 4f), but not on any of the other leaf traits (weight: $P = 0.23$: Figure 4d, length: $P = 0.42$, area: $P = 0.69$, Table 1). Annual stem length had a positive effect on leaf biomass (i.e. weight, length and area: $P < 0.05$). For leaf weight given area, the top-ranked model included only warming and icing. Leaf weight given area was not affected by icing ($P = 0.70$, Table 1) or warming ($P = 0.14$, Table 1). Model selection tables are given in the Appendix.

The model selection outcome showed that the number of catkins was sex-dependent, as the top-ranked model included sex, abundance, warming, icing, the interaction between sex and warming and the interaction between sex and icing (abundance, in addition to icing and warming, was forced to be included in the model). The number of male and female catkins decreased with experimental warming (female: $P < 0.05$, male: $P < 0.001$, Figure 4d, Table 1), with an interaction effect warming:sex (stronger negative effect in males). Flower production was reduced with less than one catkin in both sexes with warming per square (10 x 10 cm). Icing did not have a significant effect for females ($P = 0.36$) or males ($P = 0.34$). The top-ranked model for *S. polaris* abundance included icing, warming, naturally occurring ice thickness and mean NDVI. The abundance was not affected by experimental icing or warming (icing: $P = 0.18$, warming: $P = 0.31$, Figure 4g, h, respectively). *S. polaris* abundance was positively affected by natural icing ($P < 0.05$). None of the most parsimonious models included the interaction term between experimental icing and warming.

3.2 NDVI and Vegetation Structure

The top-ranked model for peak season NDVI included only icing and warming. Experimental icing increased peak season NDVI ($P < 0.001$, Figure 4k, Table 1), but the effect of experimental warming was not significant ($P = 0.27$, Figure 4l, Table 1). I tested for a possible correlation between peak season NDVI and *S. polaris* abundance and found that the relationship was not significant ($r = 0.31$, $n = 36$ plots, $P = 0.07$).

The screening of species composition based on abundances from PIM showed that the plots clustered according to blocks. Both DCA and GNMDS indicated that differences in species composition between plots were not caused by the treatments (Figure 5 and Figure 6 in the Appendix). DCA and GNMDS axes were strongly correlated (DCA1 and GNMDS2: $\tau = 0.59$, $P < 0.001$, $n = 36$ plots, DCA2 and GNMDS1: $\tau = -0.63$, $P = 6.6e{-}09$, $n = 36$ plots), but the two methods disagreed on which axis was the main axis (DCA1 and GNMDS1: $\tau = 0.21$, $P = 0.07$, $n = 36$ plots, DCA2 and GNMDS2: $\tau = 0.22$, $P = 0.07$, $n = 36$ plots).

Table 1: Model estimates (estimate ± SE) of treatment effects (experimental warming and icing) and covariates, based on the top-ranked linear mixed effect models (when warming and icing were forced to be included). Estimates for count data (i.e. the number of catkins using negative binomial distribution and abundance using Poisson distribution) are given with a log link based on generalised linear mixed effect models. The number of catkins is measured at the square level (10 x 10 cm). Abundance is measured as the number of hits using Point Intercept Method (25 intercepts).

Response variable	Intercept (Control)	Stem length	Warming	Icing	Leaf area	Natural ice	Mean NDVI
Stem length (mm)	8.20 ± 1.23	-	**-1.80 ± 0.72 (*)**	0.87 ± 0.72	-	-	-
Leaf SLA (mm^2/mg)	14.4 ± 0.6	-0.5 ± 0.3	**-1.4 ± 0.7 (*)**	-0.2 ± 0.6	-	-	-
Leaf weight (mg)	4.49 ± 0.35	**0.70 ± 0.21 (***)**	0.51 ± 0.42	-0.20 ± 0.41	-	-	-
Leaf weight for a given area (mg)	4.42 ± 0.18	-	0.30 ± 0.21	0.08 ± 0.21	**2.33 ± 0.03 (***)**	-	-
Leaf length (mm)	9.22 ± 0.34	**0.90 ± 0.19 (***)**	0.28 ± 0.35	-0.12 ± 0.33	-	-	-
Leaf area (mm^2)	59.8 ± 4.0	**7.4 ± 2.4 (**)**	1.9 ± 4.8	-2.8 ± 4.6	-	-	-
Abundance	2.31 ± 0.13	-	-0.11 ± 0.11	0.17 ± 0.12	-	**0.12 ± 0.05 (*)**	**0.19 ± 0.06 (**)**
Peak season NDVI	0.697 ± 0.008	-	0.010 ± 0.009	**0.048 ± 0.009 (***)**	-	-	-
	Intercept (Control, Female)	Male	Warming	Male: warming	Icing	Male: icing	Abundance
Number of catkins	0.28 ± 0.37	0.04 ± 0.20	**-0.64 ± 0.31 (*)**	**-1.04 ± 0.24 (***)**	-0.29 ± 0.32	0.34 ± 0.24	**0.48 ± 0.17 (**)**

Significance codes: P < 0.05 *, P < 0.01 **, P < 0.001 ***. Significant estimates in bold face

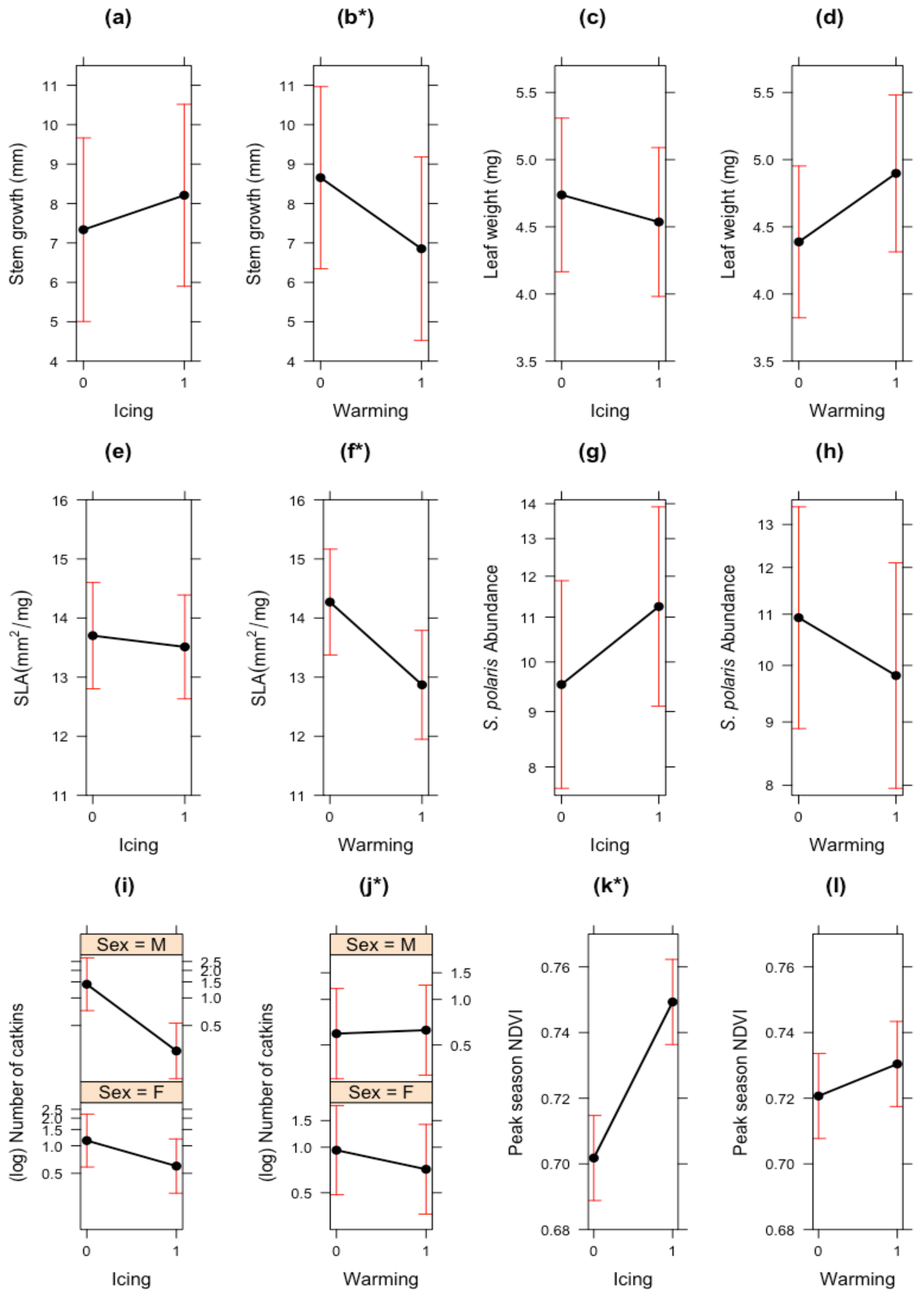

Figure 4. Treatment effect plots based on the top-ranked linear- and generalised mixed effect models in Table 1 (when warming and icing were forced to be included) for (a, b) annual stem length (unit = mm), (c, d) leaf weight (unit = mg), (e, f) SLA (unit = mm²/mg), (g, h) number of hits in PIM, (i, j) number of flowers (catkins) per square (10 x 10 cm) and (k, l) peak season NDVI (k, l). 0 = no icing or warming, 1 = icing or warming treatment. Significant effects ($P < 0.05$) ='*'.

4

Discussion

In this study, potential effects of high Arctic climate change on the dwarf shrub *S. polaris* were investigated by one year of treatment with winter icing and summer warming. The results show that increased summer temperatures, induced by OTCs, affect *S. polaris* significantly through reduced stem length (Figure 4b) and SLA (Figure 4f). A negative effect of experimental warming was found in flower production, and stronger so in males than females (Figure 4j). Experimental icing had no statistically significant effect on the parameters measured in *S. polaris*, but caused an increase in the peak season NDVI (Figure 4k). Furthermore, neither experimental icing nor warming appeared to strongly alter species composition in the moss tundra vegetation after one summer (Figure 5, Figure 6, Appendix). A limitation of the study is the short period of experimental treatment. Note that the measured responses to experimentally induced climate change are short-term responses, occurring after one season of treatment. None of the best models included the interaction term between experimental icing and warming (see model selection tables in the Appendix), indicating that there were no strong interaction effects. However, a limited sample size may be the reason why this was not found.

Correlative studies on *S. polaris* have shown that warm summers tend to produce wider tree-rings as well as increased above-ground biomass (van der Wal and Stien, 2014; Buchwal et al., 2013; Le Moullec et al., in prep). My results show reduced annual increment length with increasing summer temperatures (Figure 4b, Table 1). However, as increment length alone is a one-dimensional measure, this does not give an exact estimate of stem growth. For a more accurate measure of stem growth, more dimensions such as stem width and branching are needed. Still, if the stem growth was reduced with warming, which the results indicate, the resources may have been reallocated to become new meristem. Alternatively, the resources could have been stored in long-lived parts of the dioecious shrub, such as rhizomes of the stem or caused more branching to occur (Chapin et al., 1990).

While SLA in several dwarf shrubs has been found not to be responsive to warming in the sub-Arctic (Parsons et al., 1994), a recent study from the high Arctic (Hudson et al., 2011), found SLA in two shrubs (*Salix arctica* and *Cassiope tetragona*) to decrease with warmer temperatures. My results also suggest that warmer temperatures lead to reduced SLA, but not due to both smaller and heavier leaves. A trend towards heavier (weight) and thicker (heavier leaves for a given area) leaves was found, but estimates were not significant (Table 1). No change in leaf size (area, length) was found (Table 1). Even though the reduction in SLA to warming cannot clearly be explained based on my results, the trend could imply that SLA decreases with warming as the leaves get thicker without getter smaller. Because the experiment will be running for additionally two years, destructive sampling was restricted. Therefore, it was not possible to make a complete assessment of resource allocation within individual plants. Thicker leaves in response to warming (decreased SLA) can simply be an expression of increased plant overall growth. This could affect the flower production after multiple years, but not in the same season as flower buds are produced one or more seasons before flowering (Arft et al., 1999).

The reason for the reduction in flower production, in response to warming, is not clear, but it could possibly be a result of stress induced by the OTCs. Why there was a larger reduction in male compared to female flowers (catkins) with warming is also not clear. However, this trend has been found earlier in an experimental study on Arctic willows (Jones et al., 1997). Furthermore, differences between the sexes of Arctic willows have also been found (Crawford and Balfour, 1990). Moreover, Crawford et al. (1983) showed that leaf resistance in male and female plants differ, indicating that the sexes respond differently to some yet unidentified aspects of their environment. They report a higher range of leaf stomatal resistance to water exchange in female plants, indicating that females are less affected by water losses than males and that there is a difference between the sexes also in vegetative traits. Accordingly, the stronger effect found in *S. polaris* male flower production may be coupled with a difference in vegetative responses to warming.

With rising temperatures, photosynthetic as well as respiration rates increase. Increased photosynthesis in combination with enhanced nutrient uptake can lead to higher growth rates (Berendse and Jonasson, 1992). In our field experiment, the OTCs increased air and soil temperatures by 0.85°C and 0.98°C on average respectively, compared to the control plots. This temperature increase is considerably lower than what has been measured in other OTC-treatment studies from Arctic areas with an average increase of 1.2 - 1.8°C in air temperature and up to 5.2°C in soil temperature (Marion et al., 1997). A recent evaluation of the OTC treatment across polar and alpine regions (Bokhorst et al., 2013), found that the temperature inside the OTCs strongly correlates with irradiance, suggesting that photosynthetically active radiation (PAR) is a suitable predictor for the mean warming effect. Hence, the weak temperature increase with OTCs seen in our experiment might be a result of an overall cloudy summer with consequently low solar radiation. Despite a weak warming effect in our OTC treatment, a parallel study (Haraldsen, 2017) from the same experiment, found that with warming, some graminoids become more abundant in terms of hits in PIM. Hence graminoids could potentially cover more of the canopy, and shading could limit the solar radiation reaching the dwarf shrub *S. polaris.* This could explain the reduced SLA found in *S. polaris* since the shrub potentially received less light due to shading of other species that benefited from warming and grew taller. Furthermore, light attenuation could in the long-term negatively affect *S. polaris* (Chapin et al., 1995; Elmendorf et al., 2012) and further reduce its competitive ability (Westoby et al., 2002). Light competition in the moss tundra vegetation is however not very likely, due to low vegetation density, and presumably scant occurrence of shading.

The abundance of *S. polaris* was found to be positively affected by naturally occurring ice, which could be confounded with some other aspects of the environment. Likely, plots with more naturally occurring ice are also more concave. *S. polaris* often grows in the concavity of the landscape, which in turn could facilitate features such as greater soil moisture as well as ground ice formation in winter. Furthermore, *S. polaris* seems to be quite resistant to one winter of ice encapsulation, given that none of the traits measured had a significant effect in response to the icing treatment (Figure 4a, c, e, g, k, Table 1). In general, Arctic plants are more tolerant to anoxia than the same species from lower latitudes (Crawford et al., 1994). With frost-resistance patterns such as winter hardening (Callaghan et al., 2005), *S. polaris* should be able to protect itself from anoxic injuries. Thus, one year of winter icing does not appear to affect the growth or flower production in *S. polaris.* Nonetheless, ROS has been found to reduce the growth allocated to ring-width only in coastal sites of Svalbard (exposed to strong ROS-events) (Sandal, 2017). Following Sandal (2017), one might still expect negative effects in *S. polaris* by inducing stronger ROS-events than in our experiment.

A more productive Arctic due to increased summer temperatures has previously been found in the concept of 'Greening of the Arctic' (Walker et al., 2012; Raynolds et al., 2008; Xu et al., 2013). The results show increased peak season NDVI with warming, indicating but not significantly the same trend. Surprisingly, it was also found that with experimental icing (simulating ROS events due to warmer winters), peak season NDVI was significantly higher compared to controls (Figure 4k, Table 1). This was unexpected but consistent with the tendency that winter icing increased *S. polaris* abundance (hits in PIM, Table 1). Furthermore, analyses of the same experiment found a general tendency of delayed phenology in the plant community with winter icing, but that it tended to diminish in the later part of the season (Hovdal, 2017). The catch-up effect of delayed phenology could support my findings of the unforeseen increase in peak season NDVI, as there was an initial negative response to icing that diminished by the reach of peak season.

Within Arctic vegetation types, linear relationships between NDVI and phytomass have been found in several studies (Johansen and Tømmervik, 2014; Hope et al., 1993; Riedel et al., 2005; Spjelkavik, 2009). Because of its properties and direct relationship with photosynthesis activity, NDVI is often used to surrogate primary productivity (Sellers, 1985; Tucker and Sellers, 1986; Prince, 1991). But since photosynthesis per unit area is also a function of green biomass, and therefore is related to vegetation cover and species abundances, PIM is also commonly used as a proxy for the photosynthetic productivity. The two methods should thus not be viewed as alternative methods, but rather complementary. As *S. polaris* abundance (hits in PIM) was not significantly affected by experimental icing (Figure 4g, Table 1), it is not likely to explain the total increased NDVI during peak season. Moreover, Haraldsen (2017) found that abundance of some graminoids increased with experimental icing, which in addition to *S. polaris* abundance could contribute to the increased NDVI. *S. polaris* is a highly abundant species in high Arctic tundra communities (Bliss and Matveyeva, 1992), but it might be disadvantaged – allowing more responsive species to become more abundant. One should keep in mind that the species abundances estimated with PIM do not necessarily capture the overall picture reflected in the NDVI measure. A problem in low percent-vegetation cover such as the moss tundra vegetation is the differences in plant biomass distribution such as leaf:stem ratios, as well as plant structure, which may be expected to bias the representation of different growth form abundances by PIM (Barkaoui et al., 2013).

As expected, species seem to respond to warmer temperatures differently, and tall-growing groups tend to benefit from it the most based on Elmendorf et al. (2012), supported by the findings of Haraldsen (2017). The response to winter icing also seems to differ between species. By analysing all species abundances following the same method as described for *S. polaris*, I discovered that some of the mosses, in addition to the graminoids found by Haraldsen (2017), increase in abundance (hits in PIM) in response to experimental icing (analyses not presented). Furthermore, other species including mosses and dwarf shrubs were reduced following this treatment (analyses not presented). However, one must keep in mind that the effect sizes with the short experimental period (one year) are relatively small, and thus the results should be interpreted carefully. In the long-term one might expect to see a change in species composition in response to winter icing and warmer summers, but with a short-term study, no signs of an altered structure were found (Appendix, Figure 5, Figure 6).

While *S. polaris* appears to be affected by warmer summers, one-year winter icing did not seem to impact the species. Still, my results might be a short-term outcome of ecosystem disturbance, and thus we need to study the effect over multiple years to increase our understanding of future ecosystem-level changes in response to Arctic climate change. How winter icing and warmer summers interact on *S. polaris* is still left for future research, given that long-term responses may differ substantially from short-term responses. As this experiment is still running for two more years, one might hope this can contribute further to assess the responses in *S. polaris* in the face of climate change. The alterations in *S. polaris,* which I predict with warmer summers based on my short-term results, could cause huge implications for herbivores such as the resident Svalbard reindeer.

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7

Appendix

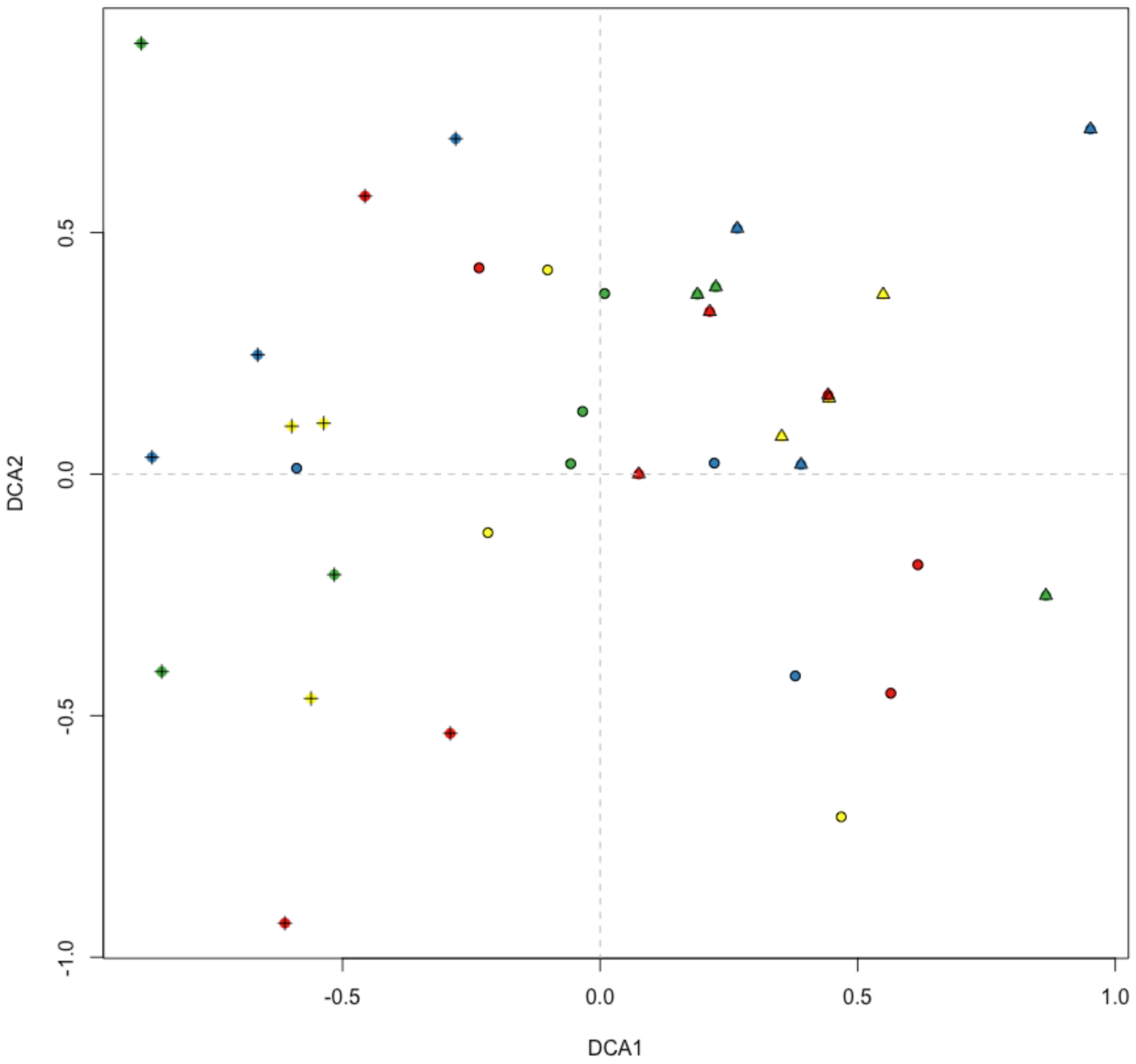

Figure 5. Detrended correspondence analysis (DCA) of plot scores. Control plots (C) = green, icing plots (I) = blue, plots treated with both icing and warming (IW) = yellow, warming plots (W) = red. Blocks illustrated with different shapes.

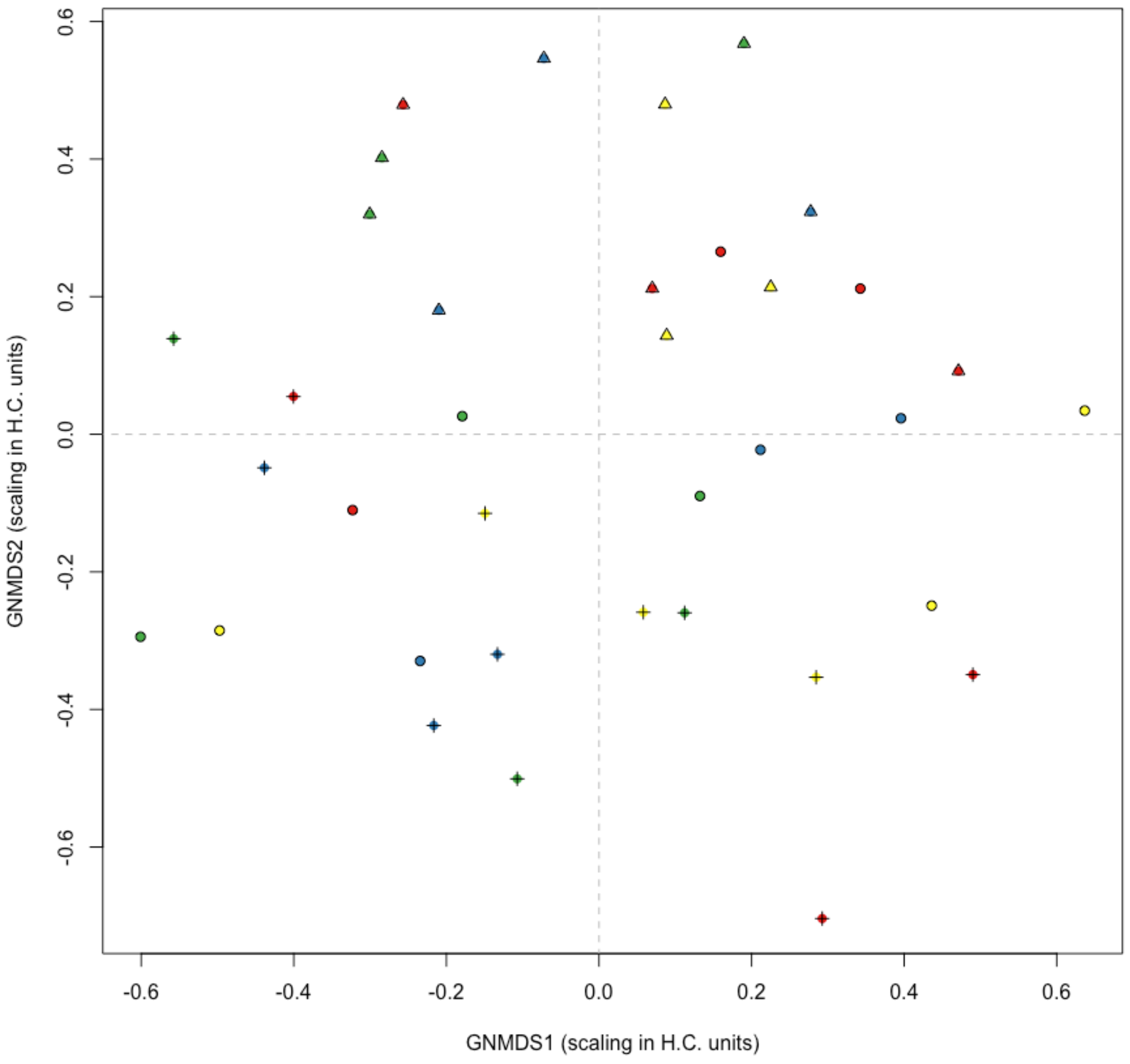

Figure 6. Global Non-Metric Multidimensional Scaling (GNMDS) of plot scores. Axes scaled in half-change units. Control plots (C) = green, icing plots (I) = blue, plots treated with both icing and warming (IW) = yellow, warming plots (W) = red. Blocks illustrated with different shapes.

Table 2: Model selection table showing best model for *S. polaris* annual stem length (mm) using a linear model (Gaussian family). Top model (italic face) without restrictions in candidate models. Warming and icing were forced to be included in the rest of the candidate models. Global model: Growth ~ Icing x Warming + Natural Ice + Soil Moisture + Abundance. I:W = interaction between experimental icing and warming. Best model marked in bold face.

Model	Icing	Warming	I:W	Natural Ice	Soil Moisture	Abundance	df	ΔAIC_c
Warming + abundance		+				+	*6*	*-0.90*
Icing + warming	**+**	**+**					**6**	**0.00**
Icing + warming + abundance	+	+				+	7	0.54
Icing + warming + natural ice	+	+		+			7	1.04
Icing + warming + soil moisture	+	+			+		7	1.26
Icing + warming + soil moisture + abundance	+	+			+	+	8	1.78

Table 3: Model selection table showing best model for *S. polaris* leaf weight (mg) using a linear model (Gaussian family). Top model (italic face) without restrictions in model selection. Warming and icing were forced into the rest of the models. Global model: Weight ~ Icing x Warming + Natural Ice + Soil Moisture + Abundance + Stem Length. I:W = interaction between experimental icing and warming. Best model marked in bold face.

Model	Icing	Warming	I:W	Natural Ice	Soil Moisture	Abundance	Stem Length	df	ΔAIC_c
Stem length							+	*5*	*-2.30*
Icing + warming + stem length	**+**	**+**					**+**	**7**	**0.00**
Icing + warming + stem length + icing:warming	+	+	+				+	8	1.22
Icing + warming + stem length + soil moisture	+	+			+		+	8	1.68
Icing + warming + stem length + abundance	+	+				+	+	7	1.70
Icing + warming + stem length + natural ice	+	+		+			+	8	2.03

Table 4: Model selection table showing best model for *S. polaris* leaf weight (mg, when taking leaf area into account) using a linear model (Gaussian family). Top model (italic face) without restrictions in model selection. Warming and icing were forced into the rest of the models. Global model: Weight ~ Icing x Warming + Natural Ice + Soil Moisture + Abundance + Stem Length + Area. I:W = interaction between experimental icing and warming. Best model marked in bold face.

Model	Icing	Warming	I:W	Natural Ice	Soil Moisture	Abundance	Stem Length	Area	df	ΔAIC_c
Area + warming		+						+	*6*	*-1.90*
Icing + warming + area	**+**	**+**						**+**	**7**	**0.00**
Icing + warming + area + icing:warming	+	+	+					+	8	0.12
Icing + warming + area + icing:warming + soil moisture	+	+	+		+			+	9	1.07
Icing + warming + area + icing:warming + natural ice	+	+	+	+				+	9	1.21
Icing + warming + area+ natural ice	+	+		+				+	8	1.22

Table 5: Model selection table showing best model for *S. polaris* SLA (mm^2/mg) using a linear model (Gaussian family). Top model (italic face) without restrictions in model selection. Warming and icing were forced into the rest of the models. Global model: SLA ~ Icing x Warming + Natural Ice + Soil Moisture + Abundance + Stem Length. I:W = interaction between experimental icing and warming. Best model marked in bold face.

Model	Icing	Warming	I:W	Natural Ice	Soil Moisture	Abundance	Stem Length	df	ΔAIC_c
Stem length + warming		+					+	*6*	*-1.90*
Icing + warming + stem length	**+**	**+**					**+**	**7**	**0.00**
Icing + warming	+	+						6	0.67
Icing + warming + stem length + icing:warming	+	+	+				+	8	1.10
Icing + warming + abundance + stem length	+	+				+	+	8	1.35
Icing + warming + natural ice + stem length	+	+		+			+	8	1.35

Table 6: Model selection table showing best model for *S. polaris* leaf length (mm) using a linear model (Gaussian family). Top model (italic face) without restrictions in model selection. Warming and icing were forced into the rest of the models. Global model: Length ~ Icing x Warming + Natural Ice + Soil Moisture + Abundance + Stem Length. I:W = interaction between experimental icing and warming. Best model marked in bold face.

Model	Icing	Warming	I:W	Natural Ice	Soil Moisture	Abundance	Stem Length	df	ΔAIC_c
Stem length							+	*5*	*-3.80*
Icing + warming + stem length	**+**	**+**					**+**	**7**	**0.00**
Icing + warming + stem length + icing:warming	+	+	+				+	8	1.90
Icing + warming + stem length + abundance	+	+				+	+	8	1.97
Icing + warming + stem length + natural ice	+	+		+			+	8	2.03
Icing + warming + stem length + soil moisture	+	+			+		+	8	2.06

Table 7: Model selection table showing best model for *S. polaris* leaf area (mm^2) using a linear model (Gaussian family). Top model (italic face) without restrictions in model selection. Warming and icing were forced into the rest of the models. Global model: Area ~ Icing x Warming + Natural Ice + Soil Moisture + Abundance + Stem Length. I:W = interaction between experimental icing and warming. Best model marked in bold face.

Model	Icing	Warming	I:W	Natural Ice	Soil Moisture	Abundance	Stem Length	df	ΔAIC_c
Stem length							+	*5*	*-3.50*
Icing + warming + stem length	**+**	**+**					**+**	**7**	**0.00**
Icing + warming + stem length + abundance	+	+				+	+	8	1.20
Icing + warming + stem length + natural ice	+	+		+			+	8	1.96
Icing + warming + stem length + soil moisture	+	+			+		+	8	1.97
Icing + warming + stem length + icing:warming	+	+	+				+	8	2.01

Table 8: Model selection table for number showing best model for *S. polaris* flowers (catkins) using a generalised linear model (negative binomial family). Top model (italic face) without restrictions in model selection. Warming and icing were forced into the rest of the models. Global model: Catkins ~ Icing x Warming x Sex + Natural Ice + Soil Moisture + Abundance. I = icing, W =warming, I:W = interaction between experimental icing and warming. Best model marked in bold face.

Model	I	W	I:W	Natural Ice	Soil Moisture	Abundance	Sex	Sex: I	Sex: W	Sex: IW	df	ΔAIC_c
Sex + abundance + warming + sex: warming		+				+	+		+		*8*	*-1.90*
Icing + warming + abundance + sex + sex:warming + sex:icing	**+**	**+**				**+**	**+**	**+**	**+**		**10**	**0.00**
Icing + warming + abundance + sex + sex:warming	+	+				+	+		+		9	0.01
Icing + warming + natural ice + abundance + sex + sex:warming + icing:warming	+	+	+	+		+	+		+		10	0.78
Icing + warming + abundance + sex + sex:icing + sex:warming + icing:warming	+	+	+			+	+	+	+		11	0.90
Icing + warming + soil moisture + abundance + sex + sex:warming	+	+			+	+	+	+	+		11	0.95

Table 9: Model selection table showing best model for *S. polaris* abundance using a generalised linear model (Poisson family). Top model (italic face) without restrictions in model selection. Warming and icing were forced into the rest of the models. Global model: Abundance ~ Icing x Warming + Natural Ice + Soil Moisture + Mean NDVI. I:W = interaction between experimental icing and warming. Best model marked in bold face.

Model	Icing	Warming	I:W	Natural Ice	Soil Moisture	Mean NDVI	df	ΔAIC_c
Natural ice + mean NDVI				+		+	*4*	*-2.30*
Icing + warming + natural ice + mean NDVI	**+**	**+**		**+**		**+**	**6**	**0.00**
Icing + warming + icing:warming + natural ice + mean NDVI	+	+	+	+		+	7	1.73
Icing + warming + natural ice + soil moisture + mean NDVI	+	+		+	+	+	7	2.72
Icing + warming + mean NDVI	+	+				+	5	2.94
Icing + warming + icing:warming + mean NDVI	+	+	+			+	6	4.33

Table 10: Model selection table showing best model for peak season NDVI using a linear model (Gaussian family). Top model (italic face) without restrictions in model selection. Warming and icing were forced into the rest of the models. Global model: NDVI ~ Icing x Warming + Natural Ice + Soil Moisture + Abundance. I:W = interaction between experimental icing and warming. Best model marked in bold face.

Model	Icing	Warming	I:W	Natural Ice	Soil Moisture	Abundance	df	ΔAIC_c
Icing	+						*4*	*-1.50*
Icing + warming	**+**	**+**					**5**	**0.00**
Icing + warming + natural ice	+	+		+			6	0.60
Icing + warming + natural ice + abundance	+	+		+		+	7	2.41
Icing + warming + abundance	+	+				+	6	2.48
Icing + warming + icing:warming	+	+	+				6	2.80