Towards rainy Arctic winters: experimental icing impacts tundra plant productivity and reproduction

Mathilde Le Moullec[1], Anna-Lena Hendel[2,3], Matteo Petit Bon[4,5,6], Ingibjörg Svala Jónsdóttir[4,7], Øystein Varpe[4,8,9], René van der Wal[10], Larissa Teresa Beumer[1,11], Kate Layton-Matthews[1,9], Ketil Isaksen[12] and Brage Bremset Hansen[1].

1 Norwegian University of Science and Technology, Dept. of Biology, Centre for Biodiversity Dynamics; 2 University of Bayreuth, Faculty of Biology Chemistry & Earth Sciences; 3 University of Freiburg, Dept. of Wildlife Ecology and Management;4 The University Centre in Svalbard, Dept. of Arctic Biology; 5 The Arctic University of Norway, Dept. of Arctic and Marine Biology; 6 Institute of Botany of the Czech Academy of Sciences; 7 University of Iceland, Institute of Life and Environmental Sciences; 8 University of Bergen, Dept. of Biological Sciences; 9 Norwegian Institute for Nature Research; 10 Agricultural University of Sweden, Dept. of Ecology; 11; Aarhus University, Dept. of Bioscience; 12 Norwegian Meteorological Institute.

Abstract

The Arctic is warming rapidly, and the rate of warming is twice as fast in winter as in summer. More frequent extreme warm spells and associated rain-on-snow events in winter can dramatically alter snowpack conditions, ultimately encapsulating the tundra vegetation in 'basal ice' for several months. As most tundra vegetation studies have focused on summer warming, potential icing effects on phenology, productivity, and reproduction remain largely unexplored. We addressed this gap by performing a pioneer field experiment in high Arctic Svalbard, simulating extreme rain-on-snow and resultant basal ice ('icing') in five consecutive winters and assessing vascular plant responses throughout each subsequent growing season. We also tested whether icing responses were modified by experimentally increased summer temperatures. Icing alone delayed early vegetative and reproductive phenology of the dominant dwarf shrub, *Salix polaris*, but with clear evidence for a 'catch-up' in terms of improved community-level primary production later in the growing season. This compensatory growth occurred at the expense of flower production and delayed seed maturation. Both the phenological delay and allocation trade-offs were associated with icing-

induced lags in thawing out and subsequent warming up of the soil, crucial in regulating plant nutrient availability and acquisition. However, experimental summer warming modified icing effects by advancing plant phenology, thus increasing primary productivity already early in the growing season, and partially offsetting negative icing effects on reproduction. Consequently, both winter and summer warming must be considered simultaneously in order to predict climate change responses of Arctic tundra vegetation. Our findings demonstrate that more frequent extreme warm spells in winter have the potential to shape key aspects of high Arctic plant communities. As we are heading towards rain-dominated Arctic winters, this calls for similar experiments in coordinated circumpolar monitoring programs across tundra plant communities.

Keywords: basal ice, compensatory growth, extreme events, open top chamber, Svalbard, *Salix polaris*, rain-on-snow, trade-offs.

1. Introduction

Global warming comes with stronger and more frequent extreme climate events, such as droughts, hurricanes and flooding, prompting research activity aimed at determining their ecological and evolutionary consequences for terrestrial biota (Grant et al., 2017; Harris et al., 2018; IPCC, 2012; Trisos et al., 2020). In the Arctic, temperatures are rising three times as fast as the global average, with particularly pronounced warming trends during winter (AMAP, in press; You et al., 2021). This has resulted in increasingly frequent and widespread winter warm spells (AMAP, 2017; Bintanja & Andry, 2017; Graham et al., 2017; Vikhamar-Schuler et al., 2016). Despite evidence for severe consequences of extreme climate events for tundra biota (Post et al., 2009) and ecosystem processes (Treharne et al., 2019), the effects of winter warm spells remain poorly understood. Indeed, most Arctic studies have exclusively focused on the effects of rising summer temperatures on tundra vegetation. This has created a large gap in our understanding of how changing conditions outside the growing season will shape the future of Arctic plant communities (Niittynen et al., 2020) – particularly critical knowledge considering the key role tundra vegetation plays for global climate feedbacks (Zhang et al., 2020).

Climate warming has long been recognized as a stimulator of plant growth in the Arctic, resulting in large-scale ‘greening’ which has mainly been attributed to shrub expansion and improved plant growing conditions (Epstein et al., 2012; Frost et al., 2019; Ju & Masek, 2016; Myers-Smith et al., 2011; Walker et al., 2006). Recently, however, the overall trend of Arctic ‘greening’ seems to have decelerated, counteracted by Arctic ‘browning’ (Berner et al., 2020; Frost et al., 2019; Myers-Smith et al., 2020; Phoenix & Bjerke, 2016; Vickers et al., 2016). Extreme warm spells in winter have been proposed as one possible cause promoting such vegetation ‘browning’ (Bjerke et al., 2017; Bokhorst et al., 2008; Bokhorst et al., 2009; Phoenix & Bjerke, 2016).

During warm spells in winter, an increased proportion of precipitation falls as rain instead of snow, often leading to extensive rain-on-snow events influencing the heat budget of the entire snowpack (AMAP, 2017; Bintanja & Andry, 2017; Bokhorst et al., 2016; Pan et al., 2018; Rasmus et al., 2018). Such mild weather and rain can lead to a complete melting of the snowpack, exposing plants to thaw-freeze cycles that may directly cause vegetation damage (Bokhorst et al., 2011; Bokhorst et al., 2009). Alternatively, and especially common in the high Arctic, the rain and resulting meltwater can collect on the frozen ground, freezes, and forms a layer of basal ice (hereafter referred to as 'icing'), up to several decimetres thick (Peeters et al., 2019; Putkonen & Roe, 2003). Low-growing Arctic vegetation can remain entirely encapsulated in this ice layer for several months, until the onset of spring. Icing has the potential for ecosystem-wide consequences by directly or indirectly affecting several trophic levels, e.g. by reducing soil arthropod abundance (Coulson et al., 2000), disrupting snow conditions for small mammals' survival and reproduction (Kausrud et al., 2008), and causing starvation-induced die-offs in large herbivores, which in turn can influence predators and scavengers (Hansen et al., 2013; Sokolov et al., 2016). Nonetheless, remarkably few studies have assessed the effects of icing on the vegetation itself.

Physiologically, icing can lead to plant cell death, either through frost damage or stress-induced anoxia metabolite accumulation from anaerobic respiration (Bokhorst et al., 2010; Crawford et al., 1994; Preece & Phoenix, 2014). In addition, icing can indirectly affect the vegetation by altering soil thermal properties (Putkonen & Roe, 2003), thus delaying plant phenology in a similar manner as late snow-melt (Semenchuk et al., 2016). A handful of studies investigated the effects of icing on vegetation in the low Arctic (Bjerke, 2011; Bjerke et al., 2018a; Preece et al., 2012; Preece & Phoenix, 2014), and short-term responses in the high Arctic (Bjerke et al., 2018b; Bjerke et al., 2017; Milner et al., 2016). In these studies, evergreen shrubs and lichens were found to be negatively affected by icing, either through

altered leaf physiology and/or shoot and individual mortality (Bjerke, 2011; Bjerke et al., 2017; Milner et al., 2016; Preece et al., 2012). In comparison, deciduous shrubs and graminoids showed higher tolerance, yet, there was still evidence of damage and biomass reduction (Bjerke et al., 2018b; Preece & Phoenix, 2014).

When organisms face sub-optimal environmental conditions, they may channel more energy into either growth or reproduction, leading to energy allocation trade-offs (Bazzaz et al., 1987; Jónsdóttir, 2011). Induced plant stress can enhance vegetative growth, thereby constraining or delaying (i.e. lagged effects) other reproductive responses (Chapin, 1991; Orcutt & Nilsen, 2000), such as flower phenology and/or number. Such allocation trade-offs are found in Arctic plants coping with shortened growing seasons (e.g. late snowmelt, Cooper et al., 2011; Wipf & Rixen, 2010), damages from e.g. herbivory (Jónsdóttir, 1991; Skarpe & Van der Wal, 2002), thaw-freeze events (Bokhorst et al., 2011), and icing. For example, in a one-year high Arctic field experiment, icing led to high mortality of apical meristems and entire shoots in the evergreen shrub *Cassiope tetragona* (Milner et al., 2016). As a result, this shrub invested more in the growth of surviving shoots the following summer, at the cost of reproductive structures, i.e., reduced flower production.

Plot-level field experiments are powerful tools to investigate fine-scale changes in plant response to simulated climate change scenarios (Bjorkman et al., 2020; Bjorkman et al., 2018; Elmendorf et al., 2012; Elmendorf et al., 2015). Here, we assess how experimental winter rain-on-snow events and subsequent icing affect productivity, reproduction, and phenology of a high Arctic tundra plant community. We also tested whether these responses were modified by summer warming. To achieve this, we simulated plot-level rain-on-snow and ice formation in winter over five consecutive years. Using a full factorial design, we also increased summer temperatures via open top chambers, following the protocol of the Arctic and Alpine International Tundra Experiment (ITEX, Henry & Molau, 1997). During each

subsequent growing season, we determined plant species and community responses to winter icing, as well as the combined effect of winter icing and summer warming. We expected icing to cause overall negative effects, i.e. to 1) delay the plants' phenology due to a delaying effect of adding 'ice' on thawing processes; 2) reduce the overall plant productivity due to shoot damage or mortality ('browning') and, possibly, delayed onset of spring; and 3) reduce the flower production due to re-allocation of resources to growth. Because of the explorative nature of our treatment combinations – i.e. no study has previously combined icing and summer warming treatments – we had no *a priori* expectations. Nevertheless, 4), we anticipated warming to reduce the overall negative effects expected from icing.

2. Methods

Study site

The experiment was located in high Arctic Svalbard (78°17`N, 16°02`E), in the valley of Adventdalen, and lasted for five consecutive years (January 2016–August 2020). The annual mean air temperature recorded at Svalbard Airport (Longyearbyen), 15 km from the study site, was -5.9 °C for the reference period 1971-2000 (Hanssen-Bauer et al., 2019), and -2.2 °C for the study period. Winter (December–February) temperature rise four to five times faster than in summer (June–August; Hanssen-Bauer et al., 2019). The interior fjord and valley areas around Longyearbyen are some of the driest in Svalbard, with an average annual precipitation of 196 mm for the reference period (Hanssen-Bauer et al., 2019) and 223 mm for the study period. In comparison to the reference period, median RCP8.5 projections for Svalbard anticipate an increase in annual temperature and precipitation of about 7-9 °C and 20-40%, respectively, towards 2100 (Hanssen-Bauer et al., 2019). The frequency of rain-on-snow events has increased dramatically since a regime shift around year 2000 (Hansen et al

2014, Peters et al. 2019). In that sense, contemporary Svalbard reflects conditions soon expected across the circumpolar Arctic (AMAP, in press; Bintanja & Andry, 2017).

Soil thermal conditions on Svalbard are linked to the underlying permafrost which warms at a rate of 1.4 °C per decade at the permafrost table (2.0 m depth), observed 6 km away from our study site between 2002–2018 (Etzelmüller et al., 2020). At the study site, the sub-surface (2 cm depth) soil temperature was on average 4.7 °C in June and 7.5 °C in July (see methodology below), the two most important months for plant growth (Van der Wal & Stien, 2014). The volumetric water content (i.e., soil moisture) is relatively low for mesic communities, drying throughout the summer season from about 45%–25% at 10 cm depth (Table S1a). Soil moisture and sub-surface temperature are strongly negatively related (Table S1b).

The plant growing season in the tundra starts immediately after the soil-thaw onset (Descals et al., 2020). Adventdalen, which is in the bioclimatic subzone C 'middle Arctic tundra' (CAVM Team, 2003), has a growing season of approximately three months, starting in mid-late May (Table 1). The plant community studied here was a mesic grass and moss-rich dwarf shrub heath, dominated by the prostrate deciduous dwarf shrub *Salix polaris* and the grass *Alopecurus borealis*. Other abundant vascular plants were the horsetail *Equisetum arvense*, the rush *Luzula confusa*, the forb *Bistorta vivipara* and the grass *Poa arctica* (Figure S1). The most abundant bryophytes were *Sanionia uncinata*, *Tomentypnum nitens* and *Polytrichastrum* spp. Nomenclature follows http://panarcticflora.org/ for vascular plants and Frisvoll and Elvebakk (1996) for bryophytes.

Experimental design

The study design followed a full-factorial randomized block design with four treatment combinations (2 levels of icing × 2 levels of warming), replicated three times within each of the three blocks (Figure 1). In summer 2015, the three blocks (150–780m apart) were

selected in homogenous mesic tundra. Within each block we chose 12 plots of 60 × 60 cm with similar communities (Figure 1). The four treatments, icing (*I*), summer warming (*W*), a combined winter icing and summer warming treatment (*IW*), and control (*C*), were randomly assigned to plots. Plots received the same treatment each year, starting in winter 2015–2016 (Table S2). This allowed us to investigate both short-term (one year) as well as longer-term (up to five years) plant responses. However, not all traits and parameters were measured in all years, hence some results are presented based only on a subset of years.

Winter icing: The experimentally formed ice was applied to *I* and *IW* plots within a period of 2–3 days in January–February (Figure 1a). Snow was carefully removed from all plots to apply the same level of disturbance, and any occurrence of natural ice was recorded. Natural ice was particularly common in 2017, with partial ice coverage occurring in all plots (3 cm average thickness). Snow was immediately placed back on non-icing (*C* and *W*) plots, while for *I* and *IW*, a 13 cm high wooden frame (60 × 60 cm) was placed around the plot and gradually filled up with cold water (for 1-3 days) until it was full of solid ice (Figure 1a), following Milner et al. (2016). Frames had no influence on the snow accumulation pattern later in winter and were removed at the beginning of snowmelt.

Summer warming: Right after snowmelt (Table S2), hexagonal open top chambers (1.4 × 1.4 m basal diagonal) were deployed over the *W* and *IW* plots following the specifications given by the ITEX protocol (Henry & Molau, 1997). To avoid confounding factors, all plots were excluded from grazing herbivores during the snow-free season using metal net cages (*I* and *C* plots) or nets on top of the open top chambers (*W* and *IW* plots; mesh-size 1.9 cm × 1.9 cm, Figure 1b).

Field measurements

Soil temperatures were recorded with iButton loggers (type DS1921G-F5, ± 1.0 °C accuracy, 0.5 °C resolution) every 120 minutes in summer and 240 minutes in winter. Loggers were

placed in all plots at depths of both 2 cm and 5 cm. In 2018, we also recorded temperatures at 10 cm and 20 cm depth (not in *IW*). We estimated the onset of soil-thaw in spring for each plot based on logger data at 5 cm depth; if soil sub-surface temperatures were ≥ 0 °C for a minimum of 10 consecutive days, the first day of this period defined the soil-thaw onset. At high latitudes, plant growth commences almost immediately upon the onset of soil-thaw (Descals et al., 2020).

To assess treatment effects on plant production, we monitored the vegetation weekly during the growing season by measuring NDVI (a proxy for plant productivity with a value from -1 to 1; Pettorelli et al., 2005). This was done at the central part of each plot (30 cm diameter) with a Skye SpectroSense2+ handheld device. NDVI typically increases in the first part of the growing season until reaching a maximum, to then drop progressively in the second part of the growing season. We considered the peak growing season to be the average day *C* plots reached the maximum NDVI (Table 1). As an additional measure of plant productivity, we measured community-level vascular plant species abundance (hereafter referred to as 'relative abundance') in the period after the peak growing season (end of July, Table 1), in 2016–2019 (Table S2). To estimate relative abundance, we used the point intercept methodology (Bråthen & Hagberg, 2004), with a 50 × 50 cm frame elevated above the canopy (~20 cm high) and with 25 evenly distributed points. The points were marked by crossings of double strings with the frame to give a 90º projection. At each point, a wooden pin of 3 mm diameter was lowered down onto the moss layer and all 'hits' of vascular plants were recorded.

To further study vegetative responses of the dominant vascular species, we collected *S. polaris* leaves (before leaf senescence, Table S2) to measure area, leaf dry weight and specific leaf area (SLA, the ratio of leaf area to dry mass, a frequently used proxy for relative growth rate (Pérez-Harguindeguy et al., 2013)). The protocol and sample size of leaf collection varied

between years (Table S2), preventing direct comparison of leaf-size traits between years, but still enabling within year comparisons of *I*, *IW* and *W* effect sizes relative to *C*. Leaves were kept moist after collection until scanned. Leaf area was measured with the program imageJ 1.48 software (Schindelin et al., 2015). Subsequently, leaves were oven-dried at 60 °C for four days and weighed on an XS204 METTLER TOLEDO scale to the nearest 0.01 mg.

To assess treatment effects on flowering frequency, the total number of flowers for the species *S. polaris, B. vivipara, A. borealis, L. confusa and P. arctica* were counted in mid-July each year (Table S2). We counted flowers in a 50 × 50 cm frame (Figure 1c), subdivided into 16 sub-squares.

To assess treatment effects on the phenology of the dominant vascular plant, we measured the most advanced vegetative and reproductive phenological stages ('phenophases') of *S. polaris* in each of 16 sub-squares per plot of the 50 × 50 cm frame. We used the following vegetative phenophases: 1) leaves starting to unfurl, 2) leaves fully expanded, 3) start of senescence, and 4) leaves fully senesced. The reproductive phenophases were 1) distinct flower buds visible, 2) buds recognisable as female or male, 3) receptive stigmas (female) and open anther releasing pollen (male), 4) stigma and anthers withered, and 5) seed dispersal. The highest number of phenological monitoring rounds took place in 2018, whereas no phenological monitoring was done in 2020 (Table S2).

Statistical analysis

We derived different metrics from the NDVI data by fitting a generalized additive model (GAM) to each plot for each year, using the repeated measurements over a growing season. We employed the function 'gam' from the mgvc package (Wood et al., 2015) in software R-3.6.3 (R Core team, 2020), fitted with restricted maximum likelihood. Model fit was good (visual interpretation and k-indices > 1), except for summer 2017 when measurements stopped before the peak growing season, i.e., they were still in the increasing

phase (Table S2). Thus, we removed 2017 from all NDVI analyses. For all other years, we predicted daily NDVI values for each plot and derived 1) the maximum NDVI value, and 2) the day-of-year when the maximum NDVI was reached. We also computed the cumulative NDVI 3) in the first part of the growing season (hereafter 'cumulative start') by summing daily values from the first day of measurements to the day when *C* plot, on average, reached the maximum NDVI, 4) in the second part of the growing season (hereafter 'cumulative end') by summing daily values from the day when *C* plot, on average, reached the maximum NDVI to the last measurement day of the season, and 5) across the growing season (hereafter 'cumulative total') by summing daily values from the first to the last day of measurements.

We used (generalized) linear mixed-effect models as the main tool to analyse our data and account for the hierarchical spatial and temporal structures of our study design, using the functions 'lmer' and 'glmer' from the lme4 R package (Bates et al., 2015). We built a separate model for each response variable, i.e., soil temperature, onset of soil-thaw, NDVI (different metrics), plant relative abundance, leaf size traits, flower number, and phenophases. The fixed effects included varied depending on whether the analysis was used to estimate treatment effect sizes (treatment was set as fixed effect), annual means ('treatment × year' interaction as fixed effect), or the average of a response over a certain time period ('treatment × day-of-year' interaction as fixed effect). The random intercept structure (i.e. variation in means between replicated units) always included the nested plot structure within blocks. It also included sub-squares nested within plots or leaves nested within shoots where relevant. Temporal replication was accounted for by including year as a random intercept (except when already set as fixed effect), and day-of-year nested within year a random intercept when measurements were also replicated within a given year. Note that we also performed a parallel analysis testing statistically for icing-warming interaction effects, i.e. using icing (0,1) and warming (0,1) as binomial predictors.

Data from soil temperature and NDVI metrics followed a normal distribution, data from plant relative abundance and flower counts followed a Poisson distribution. Leaf size traits were log-transformed. Each phenophase was converted to a binary data format to fit a logistic regression from a binomial distribution.

3. Results

Soil temperature and soil-thaw onset

The liquid water added during the simulated rain-on-snow (i.e. icing treatment) released latent heat, temporarily increasing sub-surface (i.e. 2 cm depth) soil temperatures for three days by on average 2.9 °C [2.3,3.5] (mean [95% CI], 2016–2020) in icing (*I)* and icing × warming (*IW*) plots, compared to control plots (*C*). During spring snowmelt, sub-surface soil-thaw onset was delayed by 6.0 [2.2,9.9] days in *I* and 4.4 [0.4,8.5] days in IW, while it remained unaffected in warming (*W*) compared to *C* (-0.9 [-5.0,3.1] days; open top chambers were mounted after snowmelt, Figure 2a). However, the sub-surface soil-thaw onset, and the period over which it occurred (i.e., the day-of-year range), varied considerably between years (Table 1). At 20 cm depth (data from 2018), soil-thaw onset was delayed by 9.0 [1.3,16.7] days in *I*, after staying at a constant temperature of -0.5 °C for about two weeks (i.e., 'the zero curtain period' Outcalt et al., 1990; Figure 2b). This resulted in a delay in soil temperature increase, i.e. a month-long slower increase in spring soil temperature in *I* versus *C* (i.e. entire June, Figure 2b). The presence of open top chambers increased soil sub-surface temperatures (mid-May to mid-September) by 0.8 ± 0.2 (mean ± SE) and 0.6 ± 0.2 °C in *W* and *IW*, respectively.

Vegetative responses: NDVI metrics, relative abundance, leaf size traits

The NDVI curves increased rapidly until reaching a maximum in mid-July (Table 1) and decreased slowly thereafter (Figure 3a, Figure S2). The shape of the NDVI curves varied among treatments, particularly after the maximum NDVI. This effect was captured by the NDVI cumulative metrics. For the first part of the growing season, only *IW* increased the

NDVI ‘cumulative start’, and remained high for the second part of the growing season (NDVI ‘cumulative end’), resulting in an overall increased NDVI (‘cumulative total’) across the growing season, compared to *C* (Figure 3b). In the second part of the growing season, *I* caught-up with *IW*, and thus both *I* and *IW* exceeded NDVI ‘cumulative end’ compared to *C*. NDVI cumulative metrics of *W* did not differ from *C* (Figure 3b).

The maximum NDVI timing was delayed on average by 4 [2,7] days in *I*, advanced by on average -3 [-5,0] days in *IW*, and unchanged in *W* (2 [2,7] days) compared to *C* (Figure 4a). Maximum NDVI values themselves were higher in *I* and *IW* versus *C* in the first year of treatment (2016), while this effect seemed to vanish in later years (Figure 4b). In 2020 for instance, even *C* had high maximum NDVI in comparison to other years (Table 1), reaching similar values as *I* and *IW* in other years (Figure S2). Maximum NDVI values were unaffected by *W* (Figure 4b).

Vascular plants’ relative abundance was higher under *IW* compared to *C*, largely consistent with the NDVI cumulative patterns for the entire growing season (‘cumulative total’, see above, Figure 3c). This pattern was driven by the two most abundant vascular plants, the shrub *S. polaris* and the graminoid *A. borealis* (Figure S3), which apparently had a large influence on the NDVI pattern based on among-plot correlations (Table S3). Among species, the relative abundance did not change markedly across the study period, i.e. the community composition remained overall unchanged (Figure S4).

The specific leaf area (SLA, a proxy for leaf growth rate) of *S. polaris* was higher in *I* compared to *C*, and this difference increased over the years (Figure 4c). Overall, SLA was not different in *IW* and *W* versus *C*, although variation in effect size among years was considerable (Figure 4c). Both the leaf area and dry weight tended to be lower in all treatments compared to *C*; this pattern was particularly pronounced for *I* from 2018 onwards (Figure S5).

Note that, except for SLA in 2020, no significant interaction was found between *I* and *W* in any vegetative trait, i.e. there were no strong indications of an overall modifying effect of summer warming on the response to icing (results not presented).

Reproductive response: flower production

The total number of vascular plant flowers in this mesic community was strongly reduced in *I* plots, but to some extent also in *IW* and *W*, compared to C. In 2017-2019, *I* reduced the flower production to about half of that in *C*, but it had no effect in the first and last treatment year (i.e. 2016 and 2020, Figure 4d and Figure S6). The estimated interaction effect of *I* and *W* varied strongly between years (results not presented). At the species level, *S. polaris* represented the greatest proportion of flowers and drove this overall pattern of annual variation in treatment effect, while the forb *B. vivipara* and graminoid inflorescences showed reduced flower production in all years under *I* only (Figure S6). Note that in 2020, there was a record number of flowers in the community, with more than twice the amount compared to any other study year (Table 1, Figure S6).

Phenology responses

Leaves' early phenophases (i.e., unfurling) of *S. polaris* were significantly delayed by *I*, while the timing of both leaves unfurling and fully expanding was significantly advanced (by a week) in *IW* and *W* compared to *C* (Table S4, Figure 5a-b). However, the onset of leaf senescence happened simultaneously across treatments (Table S4, Figure 5c-d), and this pattern occurred consistently in all study years (Figure S7a).

Several *S. polaris* reproductive phenophases were delayed by *I* and advanced by *IW* and *W*, compared to *C*. For female flowers, there was also evidence for a positive interaction effect between *I* and *W* (Table S4). The difference in timing was largest for the phenophase of seed dispersal (Table S4, Figure 5e-l). Seed dispersal was delayed by 5 (range at the plot-level: -2,12) days with *I*, advanced by -6 (-13,1) days with *W* and advanced by as much as -13

(-19,-6) days with *IW* (estimates for 2018, Figure 5i). Similar patterns were observed among years (Figure S7b). Furthermore, development of male flower anthers and pollen release phenophases were advanced by -4 (-7,3) days in *IW* plots (but not in *I*) compared to *C* (Table S4, Figures 5j-k), while anther senescence was rather synchronous across treatments (Figure 5l) , suggesting an extended period of pollen release of about 40% in *IW* compared to *C*.

4. Discussion:

This five-year field experiment has demonstrated how extreme winter warm spells, resulting in tundra basal ice-encasement ('icing'), affect seasonal plant growth and reproduction in a high Arctic tundra community. Icing initially delayed, but contrary to our expectations, eventually enhanced above-ground community-level productivity (Figures 3 and 4a). This was confirmed at the species level, where the vegetative phenology of the dominant vascular plant, the dwarf shrub *S. polaris*, was delayed in early summer (Figure 5a). This was, however, compensated for through an increased leaf relative growth rate (i.e., SLA, Figure 4c) and relative abundance. These observed species- and community-level delays in phenology and productivity due to icing appeared to result from later spring thawing processes, but also from an unexpected delay in soil warming in the upper active layer (Figure 2). Importantly, although the delaying effects of icing seem to be compensated for by increased growth, icing had negative effects on reproductive traits (Figures 4d and 5i). This suggests changing resource allocation trade-offs with potential life history consequences. The addition of summer warming partly counteracted icing through additive effects, but there were also indications of interaction effects on reproductive phenology. With treatments combined, the negative effects of icing on reproductive traits was reduced, while primary production was still increased. These results highlight the potentially large implications of winter warming for Arctic tundra vegetation, so far largely overlooked in both observational and experimental studies.

Increased primary production: a result of compensatory growth?

The enhanced above-ground community-level productivity due to icing contrasts with the documented 'Arctic browning' following extreme winter warm spells, a phenomenon related to damage and mortality in evergreen shrubs, and associated reductions in measured primary production (Bjerke et al., 2017; Frost et al., 2019; Phoenix & Bjerke, 2016). These differences

may be explained by contrasting overwintering strategies of the dominant growth forms in the different studies. Evergreen shrubs, virtually lacking in our study plots, maintain long-lived leaves and dormant buds well above-ground, making them more dependent on insulating snow cover and more exposed to direct damage from icing than deciduous shrubs (Givnish, 2002). Dead above-ground shoots of evergreen shrubs will remain for several years, and even if growth may be enhanced in remaining shoots (Milner et al. 2016), the net result is likely a decrease in NDVI (Bjerke et al., 2017; Treharne et al., 2020). In contrast, in our experiment, there was no sign of dead shoots on the dominant deciduous shrub *S. polaris*, likely allowing compensatory growth to enhance NDVI later in the growing season.

The icing-induced delay in the thawing of upper soil layers appeared to cause the observed phenological delay, with clear evidence for a 'catch-up' in terms of improved primary production later in the growing season, both in *S. polaris* and the vascular plant community as a whole. Soil temperature influences the availability of nutrients like nitrogen and phosphorus, which are limiting resources for plant growth in Arctic soils (Chapin, 1991; Epstein et al., 2000). In a similar mesic community, an experiment showed that soil temperature had a large influence on microbial biomass and activity, as well as plant available nutrients, thus influencing the energy transfer to the plant (Gornall et al., 2011). In the 'race' for high primary production within the reduced time window available in icing plots (i.e., due to delayed soil processes), *S. polaris* appears to compensate for delayed leaf development by increasing leaf relative growth rates (i.e. higher SLA, especially by reducing dry weight but also area, and a faster transition between phenophases from unfolding to fully expanded leaves). The overall enhanced abundance also suggests an increase in leaf number. These results agree with a laboratory icing experiment on *S. polaris* that also found reduced leaf sizes and increased leaf numbers while photosynthetic capacity remained unchanged (Bjerke et al., 2018b). This indicates that this shrub has a remarkable ability to activate dormant buds

to compensate for damage, as shown in response to herbivory (Skarpe & Van der Wal, 2002). *Salix polaris* has most of its structure and reserves below-ground, where rain-on-snow events were found to reduce its secondary growth (i.e. annual ring growth) in coastal areas of Svalbard frequently exposed to such conditions (Le Moullec et al., 2020). Therefore, larger primary growth may come at the cost of reduced secondary growth, which could alter the otherwise strong correlation between primary and secondary growth in this species (Le Moullec et al., 2019).

Although winter temperatures are rising much faster, summer temperatures are still increasing at an average rate of 0.4°C per decade across Svalbard (Hanssen-Bauer et al., 2019). As expected, summer warming partly counteracted effects of icing alone. For instance, the leaf phenology of *S. polaris* was instead advanced, increasing primary production already early in the growing season. In the low Arctic, where summer temperatures are much higher, simulated icing also advanced (rather than delayed) shrubs' early leaf emergence, explained by compensatory mechanisms from frost damaged ramets (Preece et al., 2012). Such damage was not observed (nor measured) but could also have occurred in our experiment. In addition, the increase in the relative abundance of the dominant graminoid *A. boralis* likely enhanced the primary production in the combined icing and warming treatment. In another high Arctic experiment, grasses were the growth form most rapidly responding to experimentally increased soil temperature, increasing their total live plant biomass (Brooker & van der Wal, 2003).

In contrast to evergreen shrubs, deciduous shrubs are important food for Arctic herbivores (Chapin III et al., 1996). Thus, the affected phenology and unexpected positive effect of icing on primary production may have potential implications for the whole ecosystem, such as through plant-herbivore interactions (e.g. phenological mismatches, Gauthier et al., 2013; Post & Forchhammer, 2008; Post et al., 2009), carbon fluxes (Schuur et

al., 2015) and vegetation-climate feedbacks (Zhang et al., 2020). Tundra icing may thus have counteracting effects on herbivores, directly by limiting food accessibility during winter (Forbes et al., 2016; Hansen et al., 2013), but also indirectly by affecting – and possibly increasing – the food quantity during summer.

Negative effects on reproduction: a result of trade-offs?

Compensatory vegetative growth may come at the cost of reproduction, which has been observed after thaw-freeze cycles (Bokhorst et al., 2011), snow manipulation (Cooper et al., 2011), nutrient addition (Petraglia et al., 2013), and icing of evergreen shrubs (Milner et al 2016). The reduced flower numbers in our experiment (halved in some years) could result from prioritized energy allocation to vegetative growth, if not from direct winter damage. In the first experimental year, no flower reduction occurred for *S. polaris*, suggesting that flower buds formed the previous summer survived a winter of icing. Other species, e.g. *B. vivipara* and *A. boralis*, exhibited a strong reduction in flower numbers without a lag (Figure S6). In an experiment conducted in the same valley, a record low number of flowers was associated with extreme natural rain-on-snow events in winter 2012 (Semenchuk et al., 2013). The delay in flowering phenology, and in particular seed dispersal of *S. polaris*, was likely exacerbated by a compressed growing season due to icing. Accordingly, delayed spring onset due to late snowmelt on Svalbard also resulted in delayed flower development and seed dispersal, as well as reduced flowering (Cooper et al., 2011; Karlsen et al., 2014; Semenchuk et al., 2013; Semenchuk et al., 2016).

The addition of summer warming to icing reduced the negative effects of icing on reproductive traits: flower production was less reduced (i.e. to a similar level as under warming alone) and, surprisingly, flower phenology was advanced beyond the rates obtained from warming alone. Interestingly, this suggests an interaction effect of icing and warming magnifying the advancement of phenology found under warming alone (Table S4). Advanced

phenology patterns due to warming are consistent with results of simulated summer warming at a circumpolar scale (Collins et al., 2021). Similar to Collins et al. (2021), we found a larger shift in reproductive than vegetative phenophases, resulting in a shorter period between leaf emergence and seed dispersal. This pattern was particularly pronounced under the combined icing and warming treatment, indicating a higher energy investment to reproduction, despite the also high investment to vegetative growth under icing. Our data from the extremely warm summer of 2020 also indirectly support the notion that warming may enhance the investment in both vegetative and reproductive production, as suggested by a record high number of flowers, including in control plots (Figure S6). However, the nonetheless lower flower production in warming and icing × warming plots compared to control plots possibly reflects the nutrient limitations of the system, under which vegetative growth and advanced flowering phenology are prioritized (Collins et al., 2021; Petraglia et al., 2013).

Evolutionary consequences can sometimes be expected from changing trade-offs influencing sexual reproductive structure. However, the plant species composing Arctic mesic communities are generally perennial, allowing them to wait for favourable conditions for years before reproducing sexually (Bazzaz et al., 1987). In unfavourable years, loss of those cohorts can be buffered by seed banks, although for instance seeds from *S. polaris* may be short-lived (Cooper et al., 2004). Nevertheless, *S. polaris*, as most Arctic species, also reproduces asexually by clonal growth (Jónsdóttir, 2011), limiting possible evolutionary consequences of environmental changes. This also indicates that species in such communities have developed adaptive strategies to cope with these extreme conditions. In the oceanic climate of Svalbard, winter rain-on-snow events have indeed been occurring at least for decades (Vikhamar-Schuler et al., 2016). However, their frequency and extent have increased dramatically in recent years (Hansen et al., 2014; Peeters et al., 2019), and the selection acting upon life-history traits might change when acute stress episodes from occasional icy winters

become ‘chronic’, i.e. repeated, as expected in the near future (Bintanja & Andry, 2017). Comparative ‘space-for-time’ studies including Arctic regions where rain-on-snow events are still rare could shed light on plants’ adaptive capacities to icing.

The relative impacts of winter versus summer warming.

The effect sizes (often opposite) of winter icing and summer warming treatments were similar across most traits and within the range of natural inter-annual variation, which is typically large in the high Arctic. Although the use of open top chambers only marginally increased mean summer soil temperatures, the increase was comparable to other ITEX sites in the high Arctic, where irradiance is low, restricting the warming effect (Bokhorst et al., 2013). The primary production increase under warming was therefore limited. Other tundra studies/experiments that have investigated effects of altered winter conditions, notably snow accumulation, also found similar or larger effect sizes of the winter than the summer season (Cooper et al., 2011; Niittynen et al., 2020; Wahren et al., 2005). Our study thus supports the overall insight that conditions during the ‘dormant season’ can have a substantial effect on the growth of tundra vegetation.

Climate scenarios suggest a further acceleration of warming, particularly in winter (Meredith et al., 2019), but their impacts will likely be heterogeneously distributed depending on fine-scale landscape structure (Niittynen et al., 2020). The expected complexity of conditions shaping vegetation growth patterns is supported by circumpolar studies documenting a mosaic of tundra greening and browning (Buchwal et al., 2020; Myers-Smith et al., 2020). Here, we have provided new insights by revealing some of the likely scenarios and underlying mechanisms of winter warming effects. We expect further complexity related to the timing and severity of these events, affecting the duration of ice encasement (Preece & Phoenix, 2014), with possible inter-periods of thaw-freeze events (Bokhorst et al., 2011), and the interaction with different levels of summer warming.

Conclusion and outlooks.

High Arctic environments are naturally variable, and plants have developed elaborate strategies to persist under these extreme conditions. Nevertheless, this study has shown that winter rain-on-snow, and associated tundra icing, can have similarly large impacts as summer warming on high Arctic plant communities. On the occasion of the 30-year anniversary of ITEX experiments conducted across the poles, which have provided critical knowledge regarding tundra responses to summer warming (Bjorkman et al., 2018; Collins et al., 2021; Prevéy et al., 2019), we call for the implementation of similar large-scale experiments investigating effects of winter warming, and rain-on-snow events in particular. Such a coordinated effort on long-term effects across communities, plant functional types and species is required to gain a holistic understanding of future changes in the tundra biome and its possible resistance and resilience to both winter and summer warming (Bjorkman et al., 2020). This is especially urgent given that winter warming is by far outpacing summer warming, with potentially ecosystem-wide consequences such as alteration of below-ground vegetation productivity, microorganism activity and carbon flux exchange, and cascading effects across the food web. This pioneer long-term icing experiment sets the stage for forthcoming studies to fill this fundamental knowledge gap.

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Table 1. Overview of annual mean biotic and abiotic measurements. The daily average air temperatures were recorded at the Svalbard Airport (available on https://seklima.met.no/), while the soil-thaw onset day, maximum Normalized Difference Vegetation Index (max. NDVI) metrics, and flower counts were recorded in control plots. The time of max. NDVI is interpreted as the peak growing season. DOY = Day-of-year (i.e. Julian day, where 1 = 1 January).

	2016	2017	2018	2019	2020
Soil-thaw onset day (range)	13th May (8th–22rd May)	21th May (3rd May–1st June)	10th May (6th–14th May)	30th Apr (18th Apr–20th May)	18th May (16th–22th May)
Air T°C June (range)	5.0 (3.6–6.7)	4.6 (3.2–6.5)	4.0 (2.3–6)	4.8 (3.3–6.8)	4.5 (2.8–6.8)
July (range)	9.0 (7.4–11.1)	6.9 (5.4–8.9)	7.2 (5.6–9.5)	8.4 (6.5–10.6)	9.8 (7.7–12.2)
Time of max. NDVI, DOY [CI]	16th July 197 [189;205]	NA	19th July 199 [191;207]	12th July 192 [184;200]	15th July 196 [188;204]
Max. NDVI [CI]	0.74 [0.72;0.77]	NA	0.76 [0.73;0.78]	0.76 [0.73;0.78]	0.79 [0.76;0.81]
Flower count m^2 [CI]	263 [181;345]	229 [151;288]	314 [218;409]	295 [204;386]	491 [341;642]

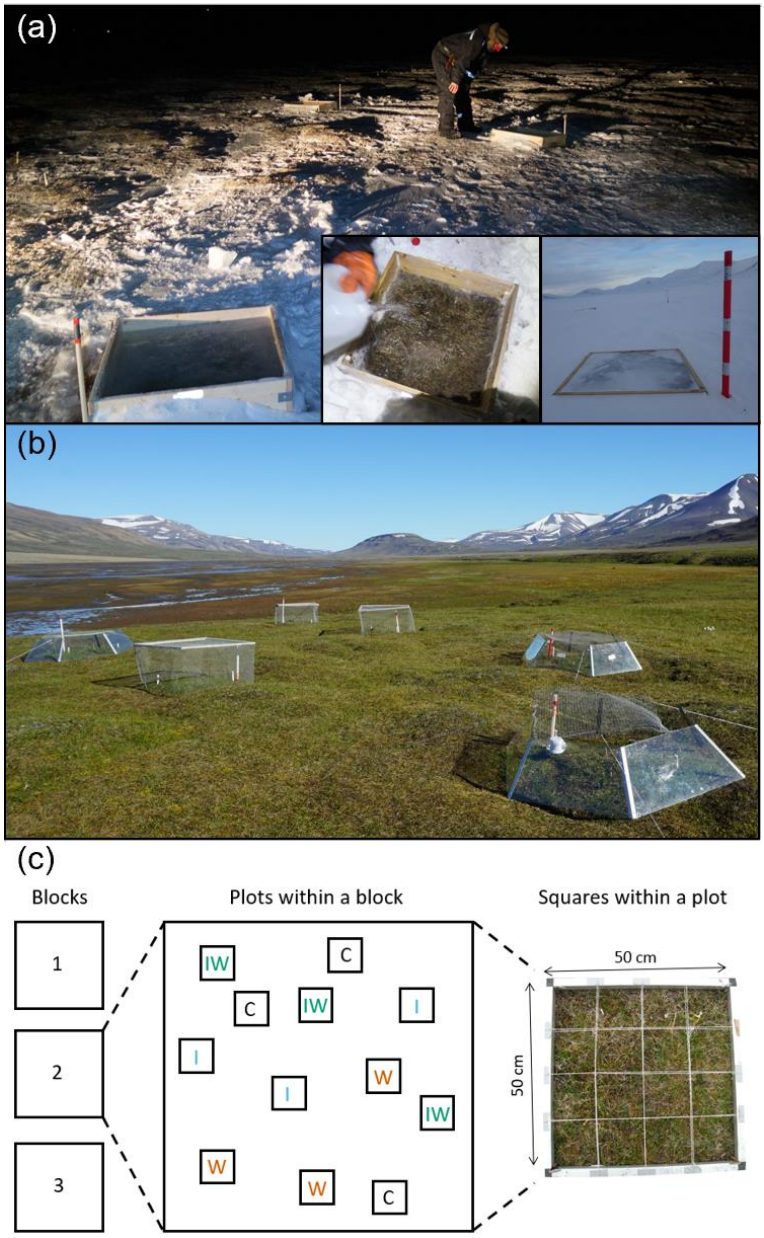

Figure 1. The experimental set up in the Adventdalen valley, Svalbard. Overview of the field site (a) in the polar night, when applying the icing treatment by filling a wooden frame with water, and (b) in summer with the open top chambers (plexiglass hexagons) simulating warming and net cages to protect against herbivory. (c) Experimental full-factorial randomized block design with the vegetation frame fitting the plot size. C = control, I = icing, IW = icing × warming, W = warming. Picture credits: Ø. Varpe and M. Le Moullec.

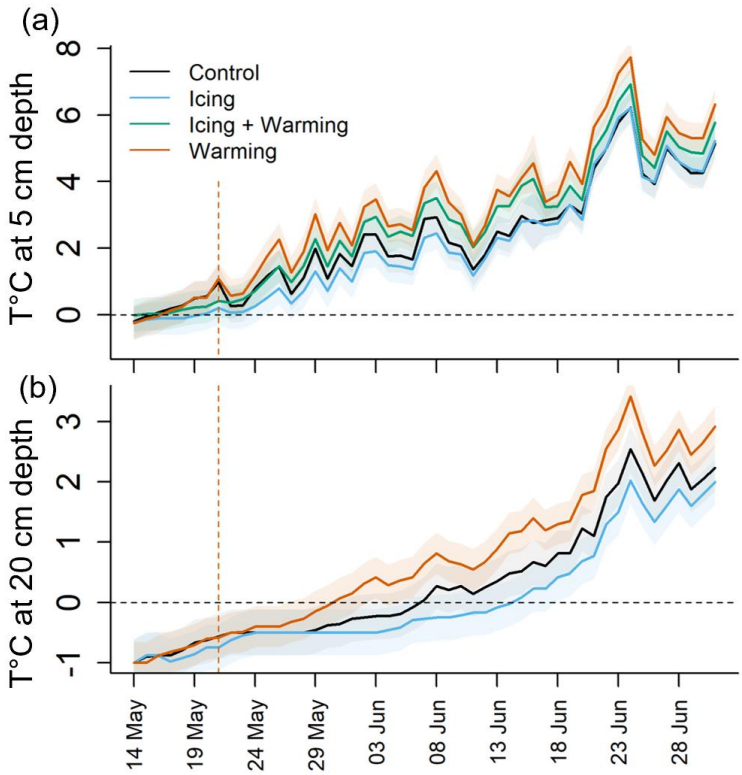

Figure 2. Daily estimates of soil temperatures during the soil-thawing period from mid-May to end of June 2018, at (a) 5 cm depth (i.e., sub-surface), and (b) 20 cm depth. Shaded areas represent 95% CIs and the orange vertical dashed lines shows the day the warming treatments started.

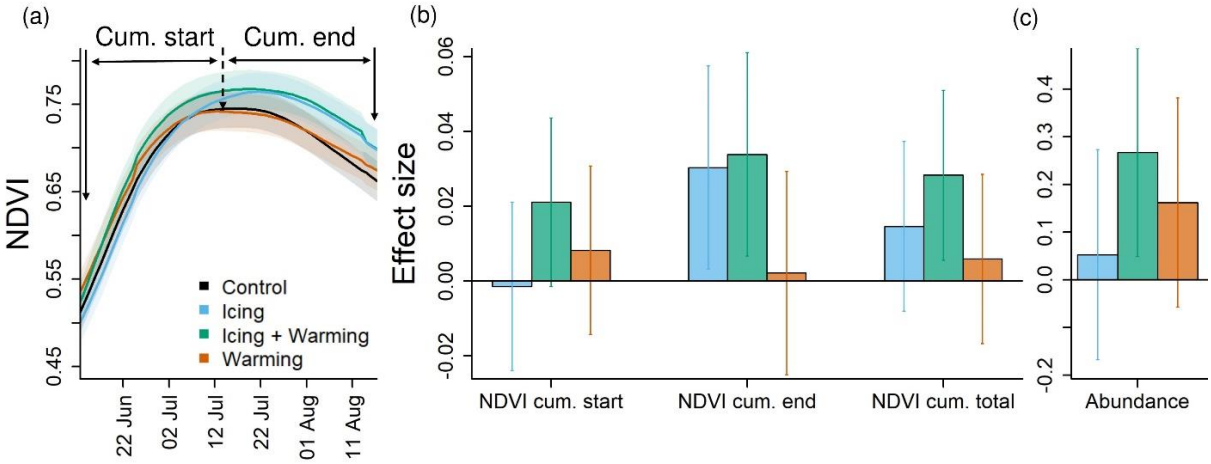

Figure 3. Experimental effects on primary productivity proxies of the tundra vegetation community (2016, 2018-2019). (a) Estimated Normalized Difference Vegetation Index (NDVI) curves and 95% CIs across the growing season. (b) Effect sizes of treatments in contrast to control plots (i.e., the reference level marked by the zero line). NDVI cum. start = NDVI cumulative start. NDVI cum. end = NDVI cumulative end. NDVI cum. total = NDVI cumulative total. (c) Relative abundance of the vascular plants assessed by the point intercept method close to the peak growing season. See Figures S2 and S3, respectively, for the NDVI curves in 2020 and for relative abundance estimates in 2017.

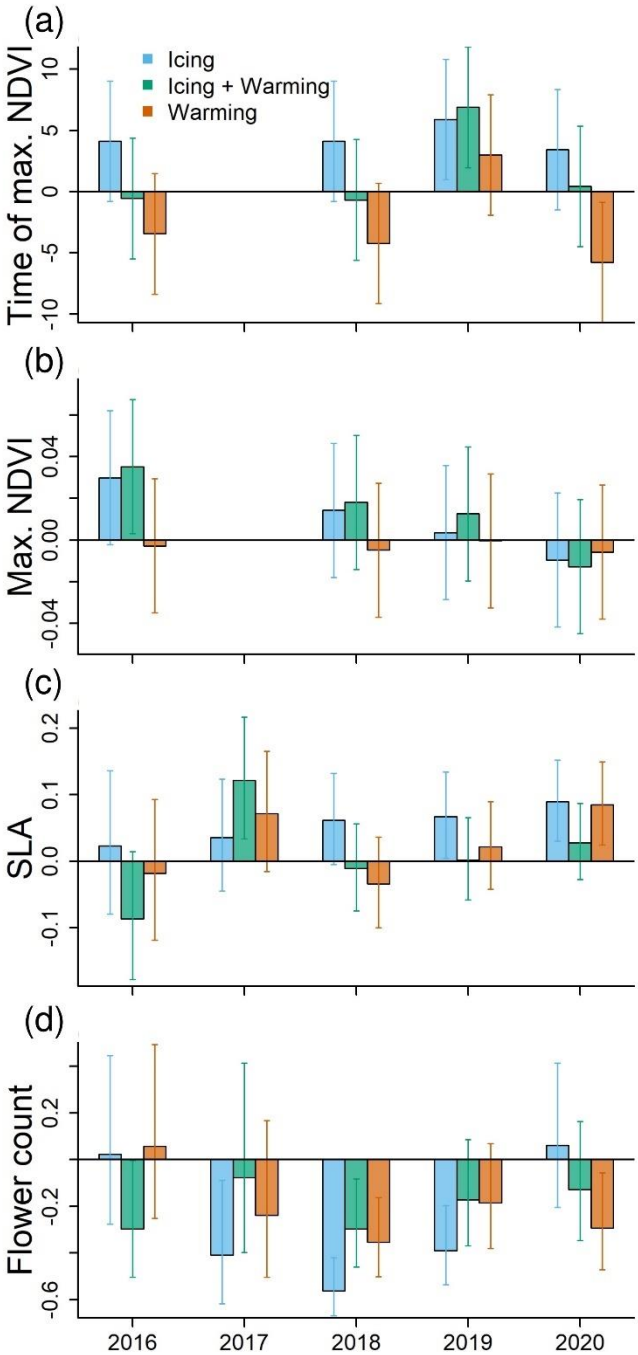

Figure 4. Effect size of treatments in comparison to controls (i.e., the reference level marked by the zero line) for the annual (a) time of maximum Normalized Difference Vegetation Index (Time of max. NDVI; in number of days); (b) max. NDVI (values from -1 to 1); (c) leaf specific area (SLA) of *Salix polaris* (log-scale); and (d) flower count per sub-square (logit-scale). The bars show the 95% CIs.

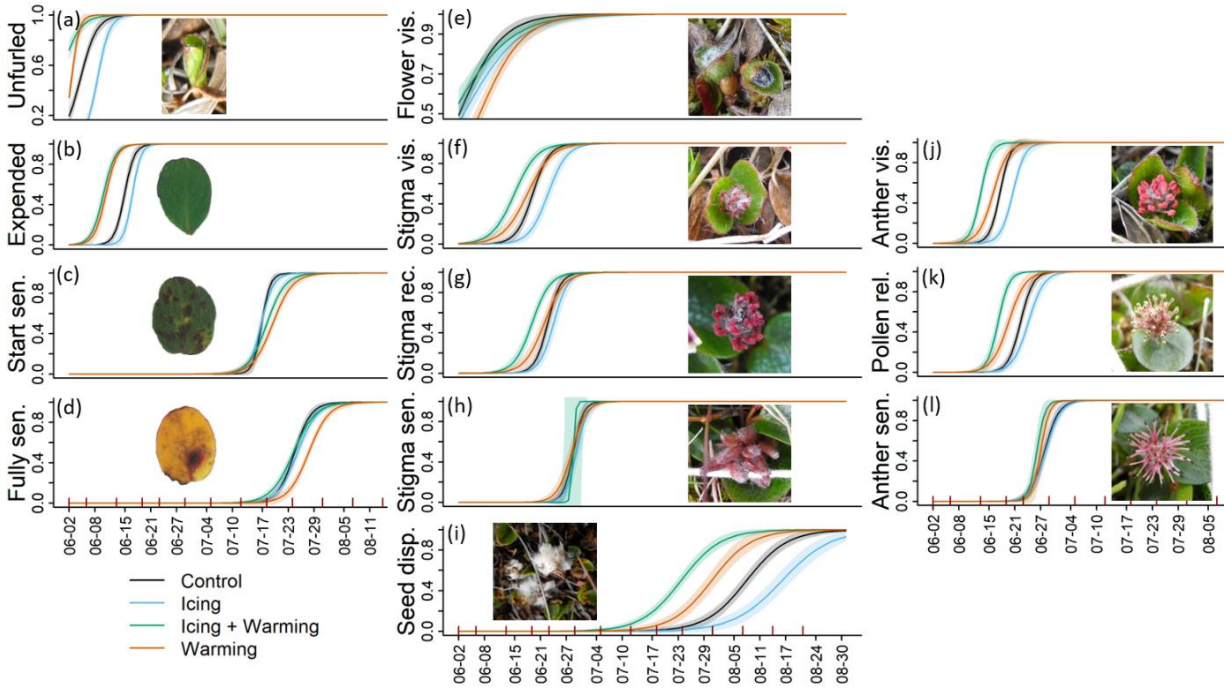

Figure 5. Probability curves of *Salix polaris* phenophases (i.e. the estimated probability of reaching a specific phase) for vegetative phases (a-d) and reproductive phases (e-i: female flowers; j-l: male flowers). Phenophases correspond to (a) leaves unfurled, (b) leaves fully expanded, (c) leaves started senescing, (d) leaves fully senesced, (e) flower visible (female or male), (f) stigma visible, (g) stigma receptive, (h) stigma senesced, (i) seed dispersed, (j) anther visible, (k) pollen released, and (l) anther senesced. Estimates are shown for 2018, i.e. the year when all phases could be estimated after the most intensive monitoring effort (for additional estimates, see Figure S7). The predicted estimates were computed with generalized linear mixed-effect models, accounting for the replicated structure of the study design (i.e., random effects), and the shaded areas represent the associated 95% CIs to the fixed-effects. Red tick marks on the x-axis represent sampling days.

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