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

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Abstract

The Arctic is the most rapidly warming region on Earth, but our understanding of ecosystem impacts is still poor. For instance, warming occurs more than twice as fast in winter than in summer, yet long-term tundra vegetation studies have almost exclusively focused on effects of the latter. In winter, more frequent extreme warm spells and associated rain-on-snow events can dramatically alter snowpack conditions and even encapsulate the vegetation in 'basal ice' for several months. Such icing effects on plant phenology, productivity and reproduction remain largely unexplored. We performed a novel five-year-long field experiment in which we simulated every winter a rain-on-snow event resulting in ice encasement of the vegetation, and assessed vascular plant responses in each subsequent growing season. We also tested whether these responses could be modified by summer warming (open top chambers). Icing delayed the dominant shrub's phenology, in particular early leaf development and seed maturation, increased community-level primary production in the second half of the growing season, but also reduced flower production. These delays and allocation trade-offs were associated with a delay in sub-surface soil thawing and soil warming in spring/summer, conditions known to influence plant root activity and nutrient availability at high latitudes. Interestingly, summer warming mitigated effects of icing alone and the combined treatment showed advanced phenology, increased primary production

across the growing season and reduced the negative effects on reproduction. In general, effect sizes of icing were as large as those observed for experimental summer warming alone. The community-level increase in primary production following icing is in sharp contrast with the recently proposed ‘arctic browning’ effect of extreme winter warm spells in evergreen shrub-dominated tundra communities. Yet, the negative effect on reproductive traits can become critical for species viability if these events become chronic. As we are heading towards a rain-dominated Arctic, our findings highlight the need for coordinated monitoring of the effects of warmer and rainier winters across tundra plant communities and growth forms across the Arctic.

Key-words: basal ice, compensatory growth, extreme events, mesic tundra, open-top-chamber, Svalbard, *Salix polaris*, tundra experiment, rain-on-snow, trade-offs.

1. Introduction

Global warming comes with more frequent extreme climate events, such as droughts, hurricanes and flooding, spurring research activity aimed at determining the short- and long-term ecological and evolutionary consequences for terrestrial biota (Bailey & van de Pol, 2016; Holmgren et al., 2006; Parmesan et al., 2000). In the Arctic, temperatures rise twice as fast as the global average and particularly markedly during winters (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 climatic events for tundra biota (Post et al., 2009) and ecosystem processes (Treharne et al., 2019), the effects of winter warm spells remain poorly understood and yet most long-term tundra vegetation studies have exclusively focused on effects of rising summer temperatures. This has left a knowledge gap on how changing conditions outside the growing season may contribute to shape the net impacts of global warming on arctic vegetation, especially considering the key role tundra vegetation plays for the global climate-feedbacks (Zhang et al., 2020).

Climate warming has stimulated plant growth in the Arctic resulting in large scale ‘greening’, which has mainly been attributed to shrub expansion and improved growing conditions for plants (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 (Berner et al., 2020; Frost et al., 2019; Myers-Smith et al., 2020; Vickers et al., 2016), with extreme warm spells in winter as one of the proposed causes, potentially even leading to vegetation ‘browning’ (Bjerke et al., 2017; Bokhorst et al., 2008; Bokhorst et al., 2009; Phoenix & Bjerke, 2016).

During warm spells in winter, 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). On the one hand, mild weather and rain can lead to a complete snowmelt, exposing plants to thaw-freeze cycles that may directly cause vegetation damage (Bokhorst et al., 2011; Bokhorst et al., 2009). On the other hand, as typical for the high Arctic, rain and the resulting meltwater can also collect on the deeply frozen ground, where it freezes, leading to the formation of 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 may be entirely encapsulated in this layer of ice for several months, with ecosystem-wide consequences by affecting soil arthropod abundance (Coulson et al., 2000) and blocking access to forage for overwintering herbivores, sometimes resulting in major starvation-induced die-offs (Forbes et al., 2016; Kohler & Aanes, 2004; Miller & Gunn, 2003; Rennert et al., 2009) which in turn fuel the arctic fox *Vulpes lagopus* populations (Hansen et al., 2013). Nonetheless, little is known about 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 could indirectly affect the vegetation through altered soil thermal properties (Putkonen & Roe, 2003) and delayed phenology, as found after late snow melt (Semenchuk et al., 2016). A handful of studies investigated effects of icing in the low Arctic (Bjerke, 2011; Bjerke et al., 2018a; Preece et al., 2012; Preece & Phoenix, 2014), or on the short-term in the high Arctic (Bjerke et al., 2018b; Bjerke et al., 2017; Milner et al., 2016). Evergreen shrub and lichens were strongly negatively affected by icing, with evidence of altered leaf physiology, 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 high-tolerance, yet, with 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 either to growth or reproduction causing pronounced 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 trait responses (Chapin, 1991; Orcutt & Nilsen, 2000), such as flower phenology and number. Such allocation trade-offs are found for arctic plants coping with shortened growing seasons (e.g. late snow melt, Cooper et al., 2011; Wipf & Rixen, 2010), damages from e.g. herbivory (Jónsdóttir, 1991; Skarpe & Van der Wal, 2002), thaw-freeze (Bokhorst et al., 2011) or, possibly, icing. For example, in a one-year high arctic field experiment, icing of the evergreen shrub *Cassiope tetragona* led to high mortality of apical meristems and entire shoots (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 an high arctic tundra plant community. We also tested whether these responses could be modified by summer warming. To achieve this, over five consecutive years, we simulated plot-level rain-on-snow and icing formation in winter. In full factorial design, we also increased summer temperature via open top chambers, following the protocol of the Arctic and Alpine International Tundra Experiment (ITEX, Henry & Molau, 1997). During each growing seasons we determined plant species and community responses to our icing and summer warming treatments. We expected icing to delay plant phenology due to later thawing out of the soil, reduce plant productivity due to shoot mortality (‘browning’) and,

consequently, reduced flowering due to reallocation of plant resources to regrowth. We expected summer warming to mitigate the icing effects.

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 years (Jan. 2016 – Aug. 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. During the reference period, winter (December-February) temperature rose four to five times faster than in summer (June-August) (Hanssen-Bauer et al., 2019). The interior fjord and valley areas around Longyearbyen are among the driest in Svalbard with 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 temperature and precipitation of about 9-13 °C and 20-40%, respectively, towards 2100 (Hanssen-Bauer et al., 2019). The frequency of rain-on-snow events has increased dramatically, with 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 Arctic (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, over 2002-2018 (Etzelmüller et al., 2020). At the study site, the soil sub-surface (2 cm depth) 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% to 25% at 10 cm depth

(Table S1a). Across the growing season, 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 the growing season of approximately three months long, 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 x 2 levels of warming) replicated three times within each of 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 similar plots of 60 × 60 cm (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 plant responses from the short-term (one year) to the longer-term (up to five years). However, not all traits and parameters were measured in all years, hence some results are presented based only on subsets 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 or nets on top of the open top chambers (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, in half of the plots (not in *IW*). We estimated the onset of soil-thaw in spring for each plot based on logger data at 5 cm depth , thereby taking the start of period for which soil sub-surface temperature had been ≥ 0 °C for a minimum of 10 consecutive days. 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 between 0-1). This was done at the central part of each plot (30 cm diameter) with a Skye SpectroSense2+ handheld device. NDVI typically increase until in the first part of the

growing season, reaching a maximum, which we considered as the day of peak growing season (Table 1), to then drop progressively in the second part of the growing season. As an additional measure of plant productivity, we measured community-level vascular plant species abundance in the period after the peak growing season (end of July, Table 1), in 2016-2019 (Table S2). We used a point intercept methodology, hereafter referred to as 'relative abundance' (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 year (Table S2), preventing direct comparison of leaf-size traits between years, but still enabling between-year comparison of *I*, *IW* and *W* effect sizes relative to C. Leaves were kept moist after collection, and scanned. Leaf area was measured with the program imageJ 1.48 software (Schindelin et al., 2015). Then, 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 in 16 sub-squares.

To assess treatment effects on 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 greatest phenological monitoring effort took place in 2018, and no phenological monitoring was done in 2020 (Table S2).

Statistical analysis

All data were analysed in R-3.6.3 (R Core team, 2020).

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), fitted with restricted maximum likelihood. Model fit was good (visual interpretation and k-indices > 1), except for summer 2017 when measurements stopped before reaching 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 then predicted daily NDVI values for each plot and derived: 1) the maximum NDVI value and 2) the day-of-year when this was reached; 3) the cumulative NDVI 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 the average control plot reached the maximum NDVI; 4) the cumulative NDVI in the second part of the growing season (hereafter 'cumulative end'), by summing daily values from the day when the average control plot reached the maximum NDVI to the last measurement day of the season; 5) the cumulative NDVI across the growing season (hereafter 'cumulative total'), by summing daily values from first to last day of measurements.

We used (generalized) linear mixed-effect models as the main tool to analyse our data, to 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 of interest, 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 to estimate treatment effect sizes (treatment was set as fixed effect), annual means (‘treatment × year’ interaction was set as fixed effect), or the average of a response over a certain time period (‘treatment × day-of-year’ interaction were set as fixed effects). The random intercept structure (i.e. variation in means between replicated units) always included the nested structure of plot within block. It also included sub-square nested within plot or leaf nested within shoot where this level of replication was 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 year.

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 thawing onset

The added liquid water during the simulated rain-on-snow (i.e. icing treatment) released latent heat, temporarily increasing sub-surface (i.e. 2 cm depth) soil temperature for three days by on average 2.9 °C [2.3,3.5] (mean [95% CI], 2016-2020) in plots being ice-encased (i.e., icing [*I*] and icing × warming [*IW*] plots), compared to control plots (*C*). During snowmelt in spring, 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., its 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 lag 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). Open top chambers presence 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* catch-up with *IW*, and thus 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 to what *I* and *IW* reached 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 unchanged (Figure S4).

The leaf specific area (i.e., SLA a proxy for leaf growth rate,) of *S. polaris* was higher in *I* compared to *C*, and this difference became greater 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 decrease in all treatments compare to C, and this consistently in *I* from 2018 and onwards (Figure S5).

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, icing (I) reduced the flower production to about half of that in C, but it had no effect in the first and last years of treatment (i.e. 2016 and 2020, Figure 4d and Figure S6). 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 of any other year of the study (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 were 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 consistently each years (Figure S7a).

Several *S. polaris* flowers's phenophases were delayed by *I* and advanced by *IW* and *W*, compared to *C*. This difference in timing was largest for the phenophase of seed dispersal (Table S4, Figure 54e-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* (Figure 5j-k, Table S4), while anther senescence was rather synchronous across treatments (Figure 5l).

4. Discussion:

This five-year field experiment demonstrates how extreme winter warm spells, resulting in tundra icing, affect seasonal plant growth and reproduction in a high arctic tundra community. Icing caused delayed, but eventually enhanced, above-ground community-level productivity, opposite to what we expected (Figure 3). This was confirmed at the species level, where the vegetative phenology (Figure 5) of the dominant dwarf shrub *S. polaris* was delayed in early summer, but more than compensated for this through increased leaf relative growth rate (i.e., SLA, Figure 4) and relative abundance (Figure S3). These observed species- and community-level delays in phenology and productivity due to simulated rain-on-snow and icing appeared to result from later soil spring thawing and delayed soil warming in the upper active layer, compared to control plots (Figure 2). Importantly, although the delaying effects of icing seem to be compensated during summer by increased growth, icing had negative effects on reproductive traits (Figure 3 and 4i), suggesting changing resource allocation trade-offs with life history consequences. Interestingly, the addition of summer warming mitigated the effects of icing alone, while still increasing the primary production. These results highlight the potentially large implications of winter climate change for arctic tundra vegetation, so far largely overlooked in both observational and experimental studies.

4.2. Icing causes delayed but increased primary production

The icing-induced delay in the thawing of upper soil layers expectedly caused the delay in early-developmental stages of the dominant vascular plant, the dwarf shrub *S. polaris*. However, the tendency for the vegetation after icing to catch-up the delay by having greater community-wide primary production later in the growing season contrasts with the documented ‘arctic browning’ following winter warm spells (Frost et al., 2019; Phoenix & Bjerke, 2016). These different observations might be explained by differences in the overwintering strategies of plants. Such ‘browning’ has mainly been associated with damage

on evergreen shrubs, which 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). The dead above-ground shoots of evergreen shrubs can mask compensatory growth (Milner et al. 2016), resulting in NDVI decrease (Bjerke et al., 2017; Treharne et al., 2020). In this experiment, without evidence of dead shoots on the dominant deciduous shrub, the compensatory growth appear to enhance NDVI.

Indirect effects of the altered soil thermal dynamics represent a likely underlying mechanism for the compensatory vegetative growth observed, both in *S. polaris* and the vascular plant community as a whole. Soil temperature influence the nutrient availability 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, 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 short time window available in icing plots (due to the delayed soil processes), *S. polaris* appears to compensate delayed leaf development by increasing leaf relative growth rates (i.e. high SLA and a faster transition between phenophases from unfolding to fully expanded leaves), reducing dry weight and area but with overall increasing abundance. These results agree with a laboratory icing experiment on *S. polaris* also finding reduced leaf size and increased leaf number, while maintaining high photosynthetic capacity (Bjerke et al., 2018b). This shrub has a remarkable capacity to activate dormant buds to compensate damage from e.g., herbivory (Skarpe & Van der Wal, 2002). The increased primary production after the peak growing season occurred despite a synchronous start of *S. polaris* leaf senescence across treatments (Figure S7a), which can be driven by cues fixed in time (e.g., photoperiod). However the rate of senescence can interacting with other

environmental factors such as temperature (Fracheboud et al., 2009; Paus et al., 1986). Regarding icing effects on below-ground (secondary) growth of *S. polaris*, annual ring growth was reduced in summers following heavy rain-on-snow in coastal areas frequently characterised by icing (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). The corresponding combination of icing and warming treatments, unexpectedly magnified primary production already early in the growing season so that icing and warming appeared additive. This can be explained by the advanced leaf phenology of *S. polaris*, but also by the increased relative abundance of the dominant graminoid *A. boralis.* Grasses were found to be the growth form most rapidly responding to experimentally increased soil temperature by increasing their total live plant biomass (Brooker & van der Wal, 2003). The extremely high summer temperature in 2020 may reflect a 'contemporary threshold' in primary production of this community, beyond which it is possibly limited by nutrient availability (Chapin, 1991; Epstein et al., 2000). In that year, the estimated maximum NDVI was very high across treatments, i.e., at the same level as in icing plots in other years (Figure S2). In addition to the heat waves that occurred in July, the soil thaw onset occurred synchronous across blocks and plots (for instance, all control plots thawed over four days instead of e.g., over one month the year before, Table 1).

In contrast to evergreen shrubs, deciduous shrubs represent the main nutritional plane of arctic herbivores in arctic regions (Chapin III et al., 1996). Thus, the delaying effect and unexpected positive effect of icing on primary production have potential implications for the whole ecosystem, at least regarding plant-herbivore interactions (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). For instance, the late summer/autumn season is when arctic and temperate large herbivores accumulate body fat, essential for surviving the following winter (Hurley et al., 2014; Loe et al., 2021). Tundra icing may thus have counteracting effects for the herbivores, limiting food availability over the winter leading to starvation, but also increasing the food quantity available in late summer.

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

Compensatory vegetative growth may come at the cost of reproduction and 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 (by about half 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 number without lag (Figure S6). In an experiment conducted in the same valley, a record low number of flowers was associated with extreme rain-on-snow events in winter 2012 (Semenchuk et al., 2013). The delay in flower phenology and in particular seed dispersal of *S. polaris* were likely exacerbated by a compressed growing season due to icing. For instance, delayed spring onset by late snow melt also showed 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).

Interestingly, summer warming mitigated the energy allocation trade-off found in icing alone. Under such conditions, plants invested simultaneously in vegetative growth and reproduction, demonstrated by the advanced flower phenology compare to controls. In particular, the timing of flowering in male *S. polaris* advanced remarkably, yet was still

followed by a synchronous senescence of the anthers, suggesting an extended period of pollen release of about 40% compared to untreated plots (Figure 5k-i). Our data for the extremely warm summer of 2020 also support that warming enhanced both the investment in high vegetative and reproductive production of control plots, as visible by a record high number of flowers (Figure S6). However, the reduction of flowers found in warming and icing × warming plots may still reflect nutrient limitation of the system under which vegetative growth is prioritized (Petraglia et al., 2013).

Evolutionary consequences are expected from trade-offs influencing sexual reproductive structure. However, the plant species composing arctic mesic communities are generally perennial, allowing them to wait for years for favourable conditions, to reproduce sexually (Bazzaz et al., 1987). In unfavourable years, loss of a cohort can be buffered by seed banks, yet, seeds from *S. polaris* may be short-lived as they showed low germination rates from seed banks (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 such communities have developed adaptive strategies to cope with these extreme conditions. In the oceanic climate of Svalbard, rain-on-snow events have indeed been occurring at least for decades (Vikhamar-Schuler et al., 2016), but their frequency and extent have increased dramatically in recent years (Hansen et al., 2014; Peeters et al., 2019). However, 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 studies from arctic regions where rain-on-snow events are still rare would shed light on plants’ adaptive capacities to icing.

4.5. The relative impacts of winter versus summer warming.

The effect sizes of winter icing and summer warming treatments were similar across most traits and in the range of natural inter-annual variation, which is typically large in the high arctic (Table 1). Although the use of open top chamber 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 experiments altering winter conditions, such as snow accumulation, also found similar or larger effect sizes of the respective winter treatment than summer warming by open top chamber (Cooper et al., 2011; Wahren et al., 2005). Our study thus supports the overall insights that the tundra vegetation growth implications of variation in conditions during the 'dormant season' can be substantial.

Climate scenarios suggest a further acceleration of winter and summer warming (Meredith et al., 2019) but their impacts will likely be heterogeneously distributed depending on landscape structure (e.g., aspect). 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 gained new insights by revealing some of the likely scenarios and underlying mechanisms of winter warming effects. We expect further complexity related to the severity of these events, such as the duration of ice encasement, repeated icing events (Preece & Phoenix, 2014) with possible inter-periods of thaw-freeze events (Bokhorst et al., 2011), and varying intensity of summer warming.

4.6. Conclusion and outlooks.

High arctic environments are naturally variable, and plants have developed elaborate strategies to persist under extreme conditions. Still, 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; Prevéy et al., 2019), we call for the implementation of similar large-scale experiments investigating effects of winter warming, notably rain-on-snow and icing events. Such a coordinated effort on long-term effects across communities, plant functional types and species, is required to gain a holistic understanding of the tundra biome's future changes 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 outpacing summer warming by far, which may have ecosystem-wide consequences, including alteration of below-ground vegetation productivity, microorganism activity and carbon flux exchanges, and cascading effects across the food web. Our pioneer long-term high arctic 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 Longyearbyen-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 (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]

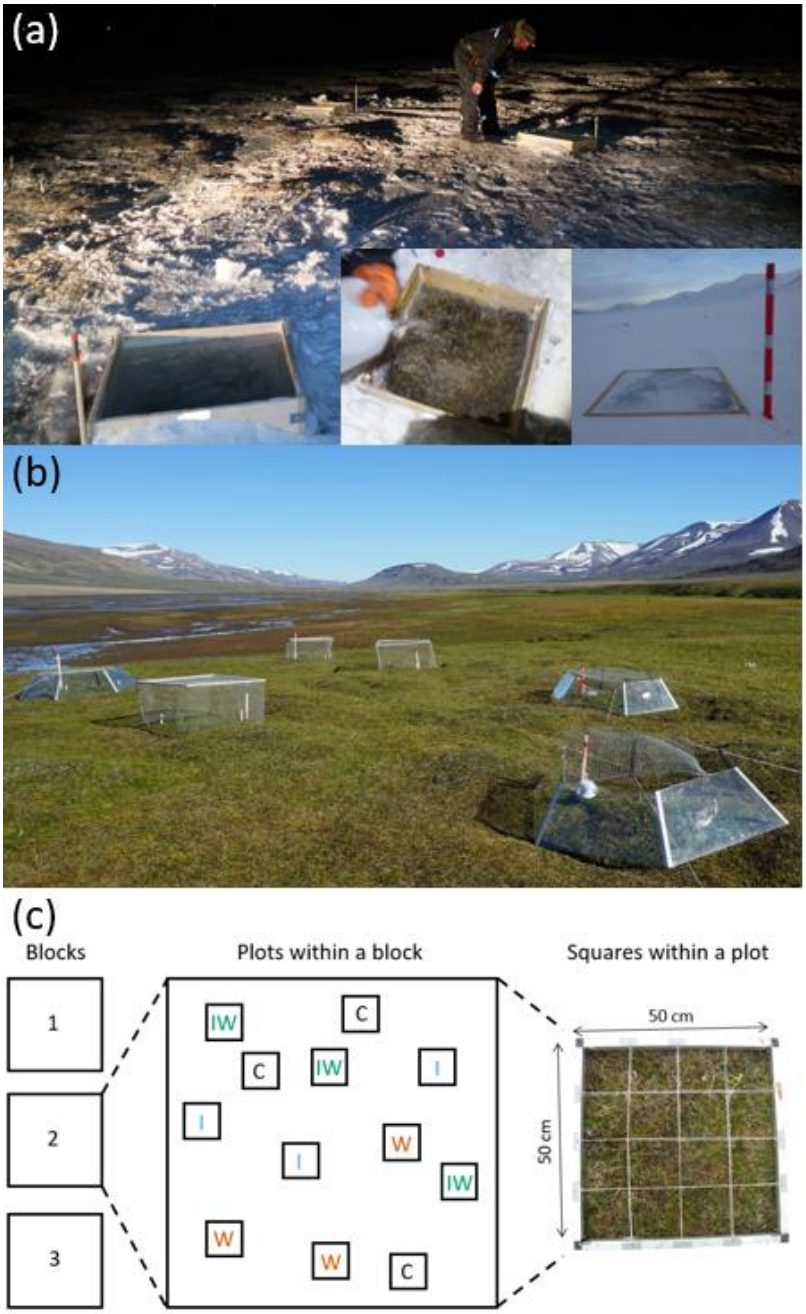

Figure 1. The experimental set up in Adventdalen, Svalbard. Overview of the field site (a) in the polar night, when applying the icing treatment by filling a wooden frame with water, and (b) in summer with the Open Top Chambers (plexiglass hexagons) simulating warming and net cages to protect against 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.

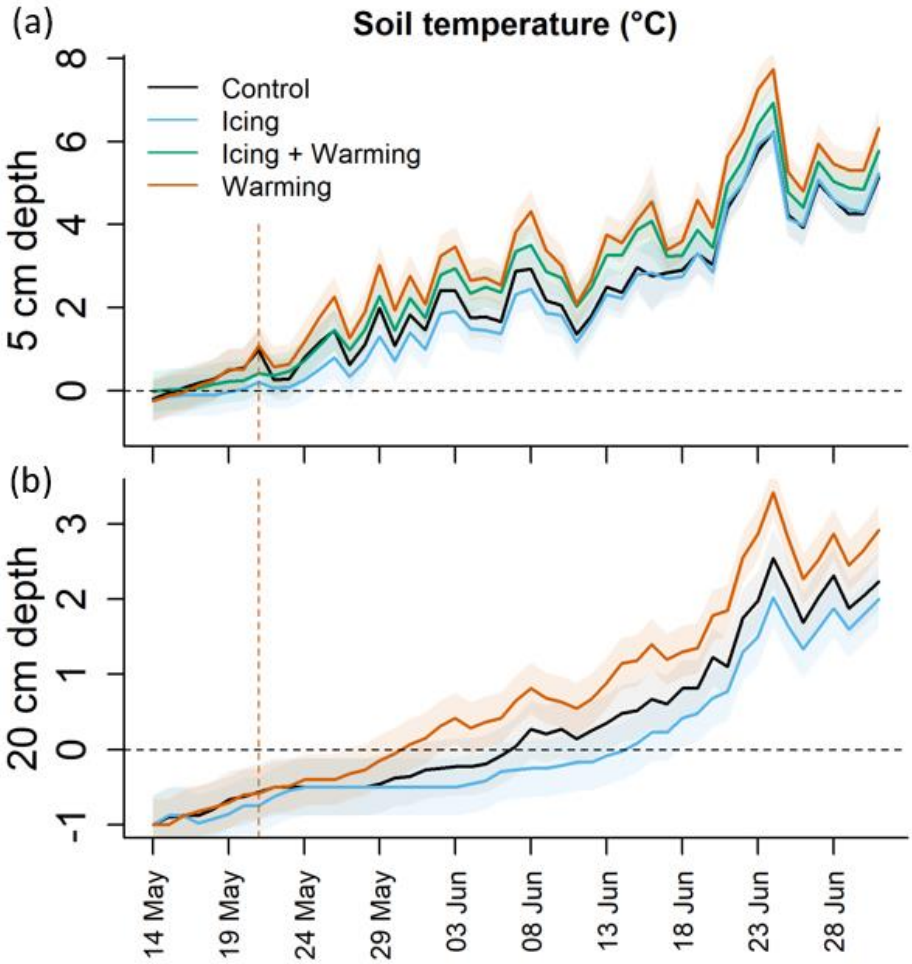

Figure 2. Daily estimate of soil temperature during the soil thawing period of mid-May to end of June 2018, (a) at the sub-surface (5 cm depth), and (b) at 20 cm depth. Shaded areas represent the 95% CI and the orange vertical dashed lines shows the day the warming treatments started.

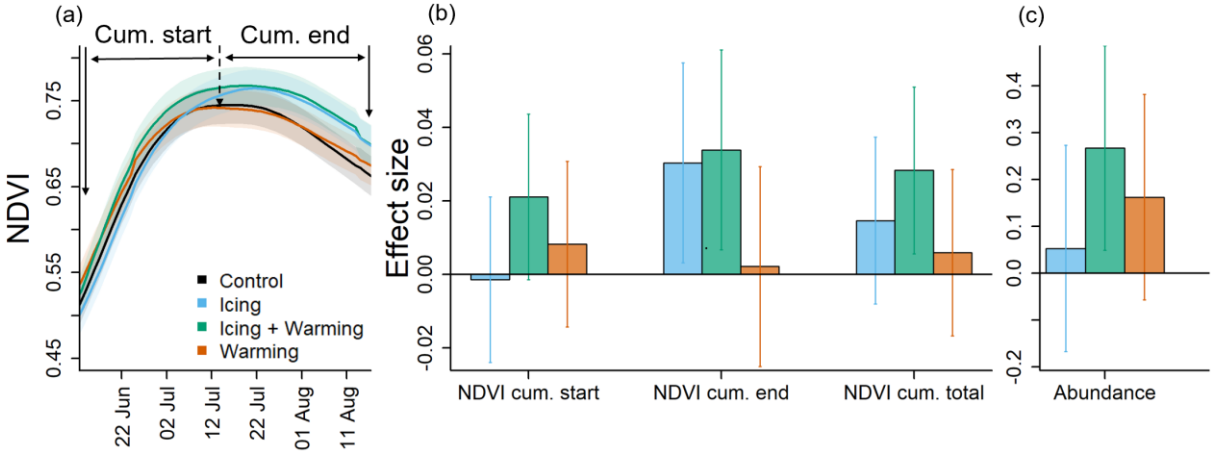

Figure 3. Experimental effects on primary productivity proxies of the community (2016, 2018-2019). (a) Estimated Normalized Difference Vegetation Index (NDVI) curves and 95% CI across the growing season. (b) Effect size of treatments in contrast to control plots (i.e., the reference level marked by the 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 point intercept methods close to the peak growing season. See Figure S2 and S3 respectively for the NDVI curves in 2020 and for relative abundance estimates of 2017.

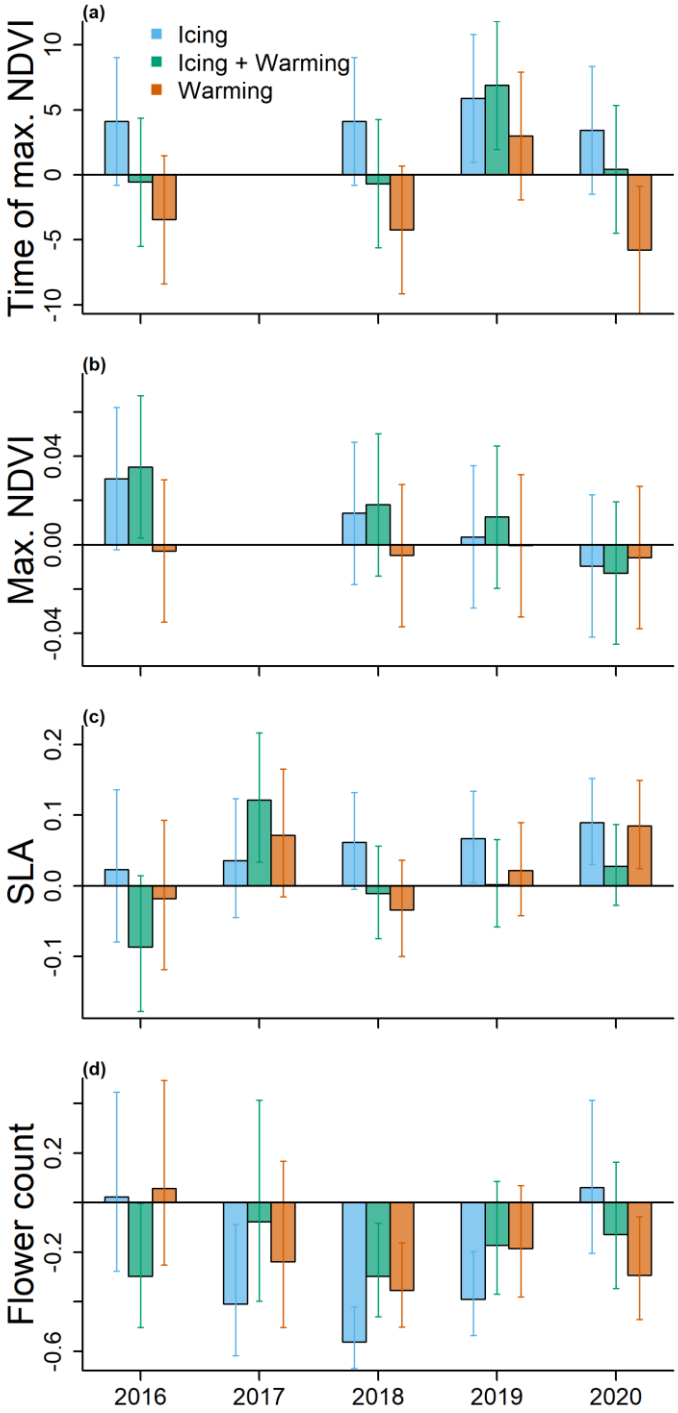

Figure 4. Effect size of treatments in comparison to controls (i.e., the reference level marked by the zero line) for annual (a) the time of maximum Normalized Difference Vegetation Index (Time of max. NDVI), in number of days; (b) the max. NDVI (values from 0 to 1); (c) the leaf specific area (SLA) of *Salix polaris* (log-scale); (d) flower count per sub-square (logit-scale). The bars shows the 95% CI.

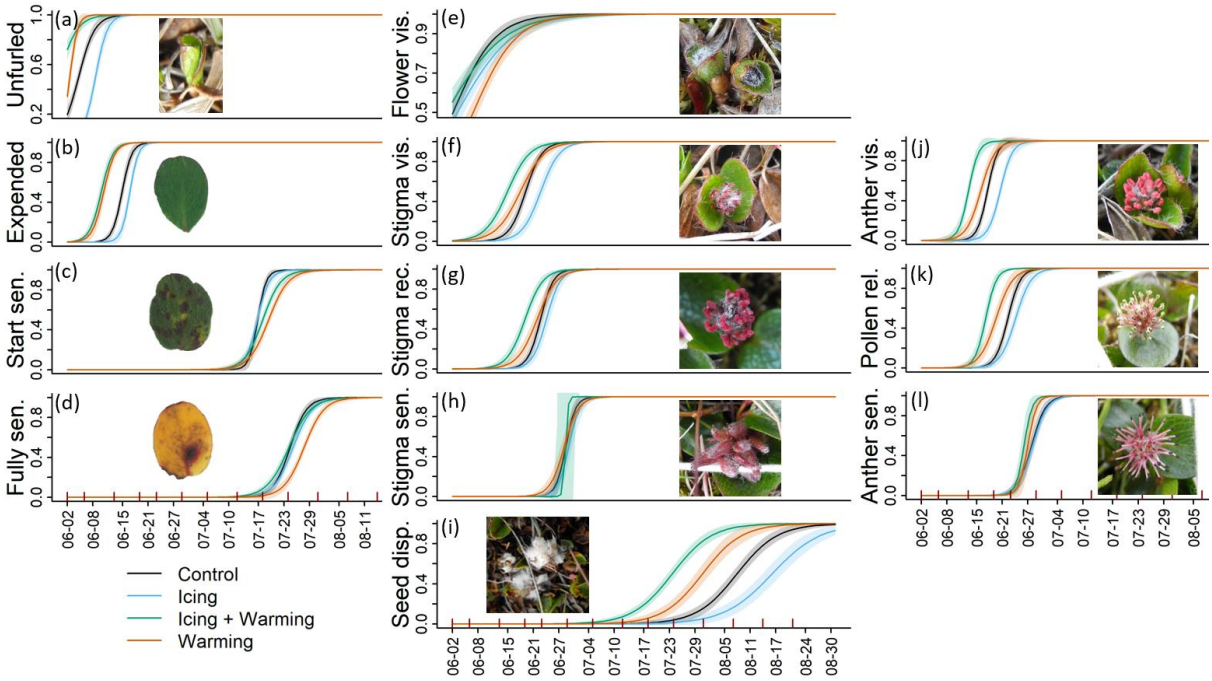

Figure 5. Probability curves of *Salix polaris* phenophases (i.e. the estimated probability of reaching a specific phase) for vegetative phases (a-d) and reproductive phases (female flowers; e-i, male flowers; j-l). Phenophases correspond to (a) leaves unfurled, (b) leaves fully expanded, (c) leaves 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, (l) anther senesced. Estimates are shown for 2018, i.e. when all phases could be estimated after an intensive monitoring effort (for additional estimates, see Figure S5). 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% CI to the fixed-effects. Red tick marks on the x-axis represent sampling days. C = control, I = icing, IW = icing × warming, W = warming.

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