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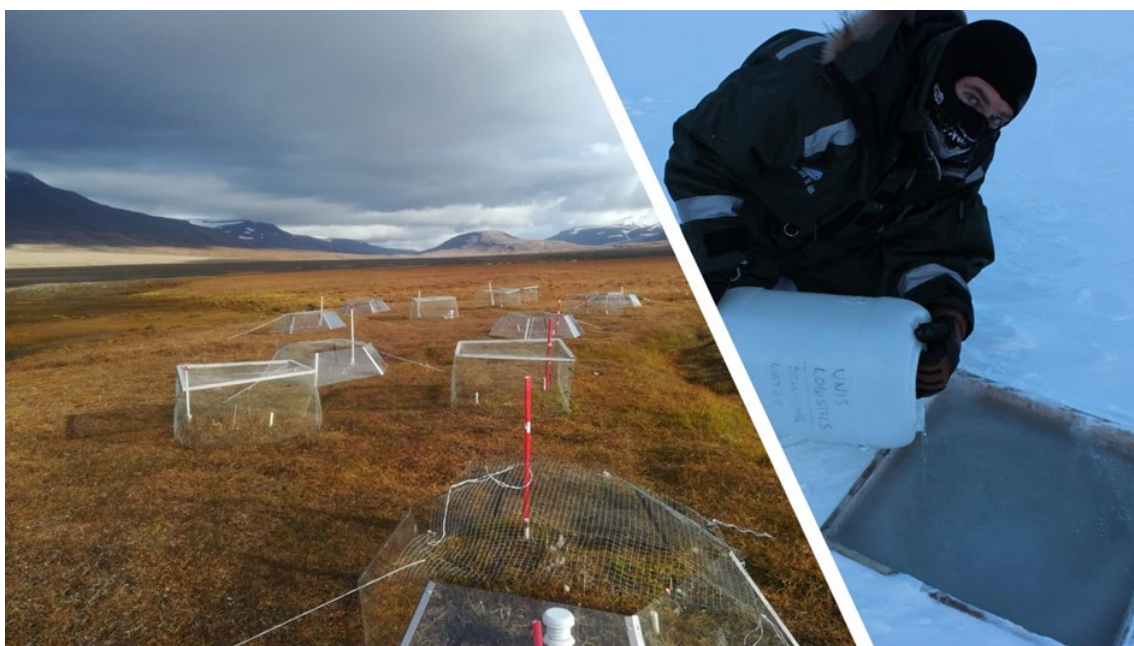
Towards rainy Arctic winters: effects of experimental icing on tundra plants and their soil conditions

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Abstract

Global warming comes with more frequent extreme climate events. In the Arctic, extreme warm spells with heavy rain-on-snow events in winter can cause dramatic changes to the snow-pack and encapsulate the vegetation in thick basal ice for several months. Ice-locked tundra can cause population crashes in Arctic herbivores by limiting food plant availability, yet specific effects on the vegetation and soil layer properties are still largely unknown. We performed a four-year field experiment in mesic communities in high Arctic Svalbard to assess effects of ice-encasement on seasonal plant growth and reproductive traits, as well as soil temperature at different depths. Simulated rain-on-snow and resultant icing were further combined with summer warming (by Open Top Chambers) in a full-factorial generalized randomized block design. Icing caused a delay in community-level productivity (measured as Normalized Difference Vegetation Index, NDVI) but also increased peak productivity in some years, compared with untreated (and warmed) plots. However, this occurred at the cost of reduced flower production in the icing plots. The delay in productivity was associated with a delay of both the thawing and spring-summer temperature increase in the upper soil active layer (especially 10-20 cm depth), which can affect plant roots. However, natural inter-annual variability in spring-summer weather, which caused shifts in spring onset (defined as when soil temperatures reach 0°C) of more than 3.5 weeks, exceeded most effects caused by icing or warming treatments. Our findings indicate that icing events mainly impact the soil-vegetation system by causing delays in seasonal development, followed by compensatory plant responses. However, they also suggest an overall resistance to such extreme events in this highly fluctuating environment. Thus, these results from high Arctic mesic vegetation – with absence of evergreen shrubs – contrast with some recent observations of "Arctic browning", which have been linked with changes in winter weather events and snow conditions.

Jan Erik Haugen	*Lars-Anders Breivik*
Disiplinary signature	Responsible signature

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by compensatory plant responses. However, they also suggest an overall resistance to such extreme events in this highly fluctuating environment. Thus, these results from high Arctic mesic vegetation – with absence of evergreen shrubs – contrast with some recent observations of "Arctic browning", which have been linked with changes in winter weather events and snow conditions.

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1 Background

Global warming comes with more frequent extreme climate events, such as droughts, hurricanes, and flooding, but little is known on the long-term ecological and evolutionary consequences for terrestrial biota (Parmesan et al., 2000, Holmgren et al., 2006, Van de Pol et al., 2017). In the rapidly warming Arctic, a higher fraction of winter precipitation falls as rain instead of snow, which also leads to an increasing frequency of heavy rain-on-snow events (Hansen et al., 2014, Vikhamar-Schuler et al., 2016, AMAP, 2017, Bintanja & Andry, 2017, Pan et al., 2018). These extreme winter weather events change the snow-pack properties dramatically, including formation of ice layers in the snow-pack or on the ground ('basal ice', Peeters et al., 2019), with potentially huge implications for biota (Hansen et al., 2013, Milner et al., 2016).

Rain can influence the heat budget of the entire snow-pack, and both rain-water and melted snow contribute to accumulation of water or slush. At the deeply frozen ground, this melt water will release latent heat, and a thick basal ice layer (sometimes called 'ground-ice') can form (Putkonen & Roe, 2003). Spatially extensive extreme warm spells with associated rain-on-snow can thus lead to basal ice formation across large areas, especially in flat terrain (Hansen et al., 2014, Peeters et al., 2019). Soil and permafrost properties are also affected (Putkonen & Roe, 2003, Isaksen et al., 2007b, Westermann et al., 2011), and during and following extreme warm spells and/or rain-on-snow on Svalbard in 2006 and 2012, permafrost temperature increased abnormally down to more than 5m depth (Isaksen et al., 2007a, Hansen et al., 2014). However, our understanding of how rain-on-snow and icing events influence thermal and hydrological properties in the soil – i.e. the layers above the permafrost that affect important biotic processes – is still poor (Meredith et al., 2019).

At high latitudes such as in Svalbard, where the vegetation is particularly short-growing, basal ice may encapsulate the entire vegetation layer for many months (Wilson et al., 2013, Bokhorst et al., 2016, Rasmus et al., 2018, Peeters et al., 2019). Basal ice thereby limits access to vegetation for overwintering herbivores, which can result in major die-offs following starvation (Miller & Gunn, 2003, Kohler & Aanes, 2004, Rennert et al., 2009, Hansen et al., 2013, Forbes et al., 2016). This effect has also been shown to cascade to other trophic levels (Hansen et al., 2013). However, except for a pilot field experiment on the evergreen shrub *Cassiope tetragona* (Milner et al., 2016), little empirical work has been done in situ on how arctic tundra plants are affected, either directly due to the ice per se or indirectly through soil processes in winter or spring-summer.

In contrast to the largely unknown effects of changing winter climate, it is well documented that rising summer temperature affects tundra vegetation by promoting growth and shrub expansion, leading to a "greening" of the Arctic (Myers-Smith et al., 2011; Ju & Masek, 2016, Piao et al., 2019). This has been studied in detail through the International Tundra Experiment (ITEX; Henry & Molau, 1997, Elmendorf et al., 2012b, Bjorkman et al., 2018). However, over large areas this greening trend has now decelerated, and increasing signs of "Arctic browning" have been documented (Bjerke et al., 2015, 2017, Epstein et al., 2015, Bokhorst et al., 2016, Ju & Masek, 2016, Phoenix & Bjerke, 2016). On the high Arctic Svalbard archipelago, Vickers et al. (2016) found a declining trend in the positive correlation between summer temperatures and primary production, measured from satellites as the annual maximum Normalized Difference Vegetation Index (NDVI). One possible explanation for this is that increased frequencies of extreme warm spells, rain-on-snow, and icing in winter have, at least in part, counteracted the response to improved plant growing conditions in summer. Tundra ice-encasement has also been proposed as one of the potential causes of observed vegetation browning, as extensive plant damage and mortality was observed in sub-Arctic heath communities (as well as botanical gardens) following such events (Bokhorst et al., 2011, Phoenix & Bjerke, 2016; Bjerke et al., 2017, 2018). Physiologically, ice-encasement can lead to plant cell death, either by frost damage or because of stress-induced and anoxia metabolite accumulations (Gudleifsson, 1997, Crawford et al., 1994, Bokhorst et al., 2010, Preece & Phoenix, 2014). Hence, ice-encasement prevents gas exchange and sets the plant in anoxic conditions (Crawford et

al., 1994). Anoxic-tolerance seems to increase with latitude (Crawford et al., 1994) but is also species-specific (Preece et al., 2012, Preece and Phoenix, 2014, Milner et al., 2016, Bjerke et al., 2018). For example, in the mentioned field experiment in Svalbard (Milner et al., 2016), encasing plots of shrubs in basal ice resulted in high mortality of apical meristems and entire shoots. As a result, plants invested more in the growth of surviving shoots the following summer, and at the cost of reproductive structures, i.e. lower flower production. Such shoot mortality and compensatory growth was not observed in a sub-Arctic icing experiment on the shrubs *Vaccinium uliginosum*, *Vaccinium vitis-idaea* and *Empetrum nigrum*, but there was leaf damage in *V. vitis-idaea* and a strongly reduced berry production in *E. nigrum* (Preece & Phoenix, 2014). Nonetheless, even if some growth or reproductive traits were affected, an overall high tolerance to experimental icing was documented (Preece & Phoenix, 2014, Bjerke et al., 2018).

Here, we present results from a four-year field experiment (2016-2019) in Svalbard, a project financed by the Svalbard Environmental Protection Fund. The experiment was designed to study the effects of heavy rain-on-snow and subsequent basal ice formation on soil thermal properties and tundra plant species in mesic habitats. Simulated rain-on-snow and icing was combined with experimental summer warming by Open Top Chambers in a full-factorial generalized randomized block design. This experiment enabled us to track potential effects of basal icing on seasonal plant productivity patterns and reproductive traits, and further link these changes to potential modifications of soil properties.

2 Study site

The experiment was located in high Arctic Svalbard, in the valley of Adventdalen, near Longyearbyen (78°17`N, 16°02`E). The annual temperatures recorded at Svalbard Airport/Longyearbyen are on average -5.9°C for the period 1971-2000 (Hanssen-Bauer et al., 2019). For Svalbard Airport/Longyearbyen the linear trend indicates an increase in mean annual temperature of 3.7 °C during the latest 118 years, which is about three times the estimated global warming during the same period. The trend is statistically significant (5% level) for all seasons. For the period 1971-present, the linear trend is 1.0 °C/decade (Hanssen-Bauer et al., 2019). For Svalbard Airport, the (statistically significant) centennial trends for annual precipitation show a linear increase of 3 - 4% per decade, and seasonal trends are highest for autumn (Hanssen-Bauer et al., 2019). The strongest temperature increase happens in winter, and rain-on-snow frequency has therefore increased (Hansen et al., 2014). The plant growing season is 2-3 months long in Adventdalen and usually starts around end of May or early June. The bioclimatic zone is the middle Arctic tundra (Jónsdóttir 2005), and the mesic community studied here contains vascular plant species such as the dwarf shrub *Salix polaris*, the forb *Bistorta vivipara* and the graminoids *Poa arctica*, *Alopecurus borealis* and *Luzula confus*a. The dominant bryophytes are *Sanionia uncinata*, *Tomentypnum nitens* and *Polytrichastrum* spp. Lichens are rare. The soil moisture is relatively dry for mesic communities, drying throughout the summer season from about 30 % to 40 % moisture level.

The permafrost on Svalbard is sensitive to changing climatic conditions and in particular to rising air temperatures and changing snow regimes. Higher permafrost surface temperatures supply a significant amount of heat to the deeper permafrost. This leads to a substantial increase in permafrost temperatures not only at the surface but also at depth. In 1998, two permafrost boreholes (15 and 102 m deep) were drilled on Janssonhaugen (Isaksen et al., 2000), approximately 10 km east from the experiment site. The boreholes were established for long-term permafrost temperature monitoring. Since the Janssonhaugen permafrost measurements started in 1998, mean annual

temperature profiles for the past 20 years show a significant change, with warming rates of more than 1 °C/decade at 10 m depth (AMAP, 2017). Similar warming rates are also observed at other monitoring sites on Svalbard, from Kapp Linne at the west coast, to gentle mountain slopes in Endalen, and mountain plateau at Breinosa (Hanssen-Bauer et al., 2019). Lower warming rates are observed at some low-land sites outside Ny-Ålesund and Longyearbyen. Differences between sites are attributed to variations in snow cover, ground ice contents, soil and bedrock type and the degree of continentality (Christiansen et al., 2018). The results clearly show that rather warm permafrost occur in some low-land areas of the Svalbard landscape.

Active-layer thickness (ALT) responds more to the shorter-term variations in climate than does deep ground temperature (AMAP, 2017). Records of ALT therefore exhibit greater interannual variability, primarily in response to variations in summer temperature. Nevertheless, observations from Janssonhaugen show a significant increase in ALT during the past 20 years (Figure 1). The extreme warm year 2016 clearly stands out in the observational record for the near surface permafrost temperatures. The years 2015-2019 all rank as the thickest active layer measured since measurement began in 1998.
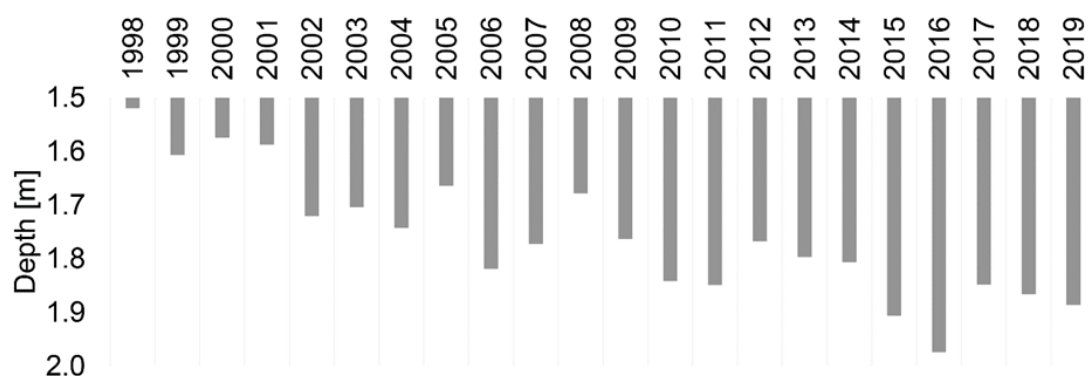

Figure 1 Maximum active layer thickness on Janssonhaugen based on interpolation of daily 0-isotherm (updated from Isaksen et al., 2007b).

3 Methods

3.1 Experimental design and treatments

The study design followed a full factorial block design. Three blocks, 150-780m apart, were selected in summer 2015. Each block contained 12 plots of 60 x 60 cm, and treatment was randomly assigned to plots (Figure 2). Treatment categories were basal ice (I), hereafter referred to as "icing", summer warming (W), a combined winter icing-summer warming treatment (IW), and control plots (C). The icing treatment was applied for four winters, starting in winter 2015-2016, in January-February. Snow was carefully removed to place a 13 cm high wooden frame fitting the plot dimensions. Following Milner et al. (2016), each wooden frame was progressively filled up with cold water mixed with snow, repeatedly over a couple of days, until it was full of solid ice (Figure 2). Frames were removed at snowmelt time. Right after snowmelt, hexagonal Open Top Chambers (OTCs) (1.4 x 1.4 m basal diagonal) were deployed over the warming (W) and icing-warming (IW) plots following the specifications given by the International Tundra Experiment (ITEX; Henry & Molau, 1997, Marion et al., 1997, Molau & Mølgaard, 1996). To avoid confounding issues, all plots were excluded from grazing herbivores during the snow-free season using metal net cages or nets on top of the OTCs (mesh-size 1.9 cm x 1.9 cm).
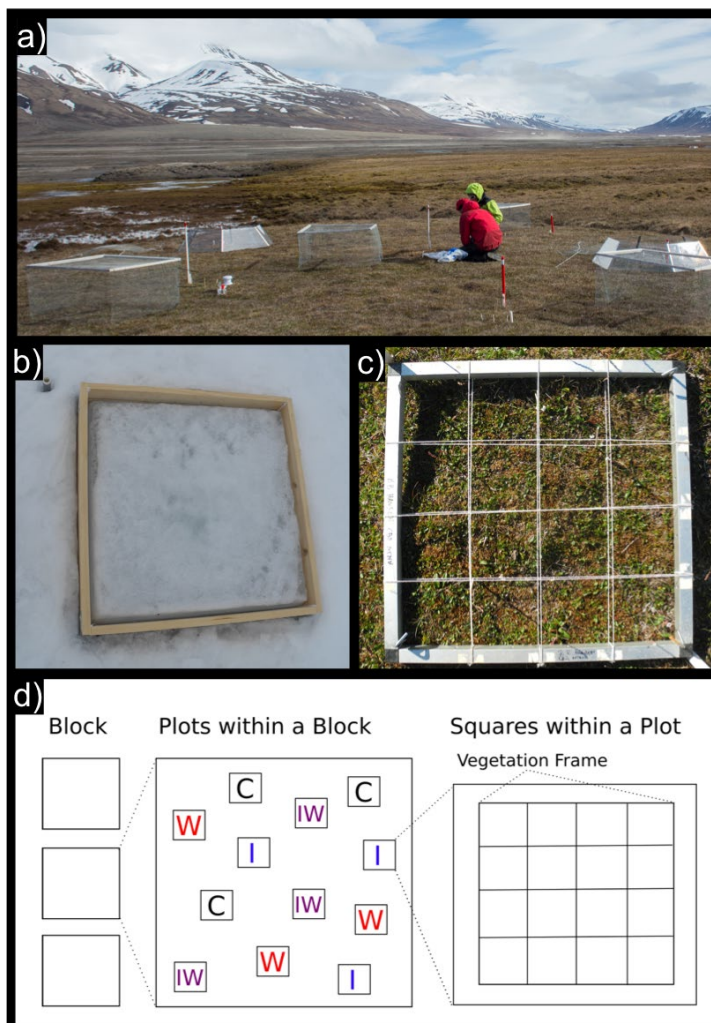
Figure 2 The Experimental Design. (a) Field site of one of the experimental blocks in the valley of Adventdalen, Svalbard. Plots of all treatments were protected against herbivores with net cages and the plexiglass hexagons are the Open Top Chambers simulating warming. (b) The wooden frame enables the experimental ice encasement of the vegetation. (c) The vegetation frame used for the flower counts. The vegetation was monitored in the 16 squares of each plot using the vegetation frame. (d) Illustration of experimental design. In total 36 plots were established within 3 blocks. Treatments included Icing (I), Warming (W), and combined treatment plots (IW). Every block included 3 controls (C).

3.2 Field measurements and analysis

In winter, plots were visited twice for snow measurements and to record potential presence of natural basal ice at the plot level. Ibutton loggers (type DS1921G-F5, with an accuracy of ± 1.0°C and resolution of 0.5°C) recorded temperature constantly at the sub-surface level (-2 cm) and at 5 cm depth in all plots in the experiment. The recording frequency was 120 minutes in summer and 240 minutes in winter. Over the winter 2017/2018 and the following summer, loggers were also placed at 10 and 20 cm depth, recording every 240 min.

Summer measurements consisted of weekly repeated measurements of selected variables, as well as measurements taken approximately at the peak of the growing season. During the weekly rounds, we measured (1) soil moisture with a theta probe (Handheld HH2, 1% accuracy) in five spots per plot, (2) Normalized Difference Vegetation Index (NDVI) with a Skye SpectroSense2+ hand-held meter, placed to cover a circumference of 30 cm centered on the plot, and (3) phenology measurements of vegetative and reproductive structures (not presented in this report, but see Hendel, 2019). Each mid-July, when flowers from all common vascular plants were opened, we counted the total number of flowers for dominant species with a 50 x 50 cm frame (centered in the plot) subdivided in 16 sub-squares (Figure 2c). Shortly after the peak growing season, biomass of each species was quantified with point intercept methods (Bråthen et al., 2004), in a 50 x 50 cm frame elevated above the canopy and with 25 intercepts (Figure 3). The intercepts were marked with double strings to give a 90° projection to record all hits down to the moss layer with a thin wooden pin.

We used linear mixed-effect models as the analytical approach to estimate effect sizes while accounting for sampling replication in time and space. The fixed effect was the variable of interest, i.e. soil temperature/moisture, NDVI, biomass or community-weighted mean flower count. The random intercept structure (i.e. variation in means between replicated units) always included the nested structure of plots within a block (and sub-plots within a plot when appropriate). Accordingly, to obtain averaged estimates over the season, we used day of year as a random effect and/or for averaged estimates over the entire study period, the random structure included year. The average number of flowers per plot was weighted by the biomass (from the point intercept method), for each species respectively. The sum of these weighted means gave the

community-weighted mean flower count at the plot level, which was further analyzed with linear-mixed effect models.

Figure 3 The point intercept method was used to measure the relative biomass after peak growing season.

4 Results & Discussion

4.1 Soil temperature and permafrost thermal responses

In the experiment, the added liquid water, derived from the icing treatment, released latent heat that increased the below soil temperatures (Woo et al., 1982, Putkonen and Roe, 2003, Westermann et al., 2011). Due to relatively thin snow cover and limited time of added water, the effects of latent heat did not last for many days. The soil below the icing treatment then cooled rapidly. A couple of weeks after the icing treatment, soil temperature in icing plots had slightly lower temperatures than in non-icing plots (Figure 4A). The thermal properties of the basal ice are different from the snow; basal ice has 4 to 10 times higher thermal conductivity than snow (Westermann et al., 2011). The snow cover in the non-icing plots insulated the soil, and the snow cover protected the ground surface from heat loss (Williams & Smith, 1989).

The temperature difference between icing and non-icing plots disappeared in April as the soil temperatures rapidly increased due to the infiltration of liquid water (due to snow melt) through the snow cover. However, in late spring, at the period of snowmelt, ice cover delayed the soil temperature increase, which was especially notable in deeper soil layers (10-20 cm, Figure 5). Consequently, the snow/ice melting day at the sub-surface was delayed by icing by 1.4 ± 2.1, 2.5 ± 1.7 and 3.6 ± 1.7 days in comparison to control plots, for the years 2016 – 2018, respectively (Figure 6). We should keep in mind that these delays are magnified deeper in the active layer (Figure 5), but data at several depths were unfortunately not available across years. Nonetheless, annual variation in the sub-surface soil temperatures was huge, with snow-ice melt occurring approximately 20 days later after the rainy winter in 2017 compared to the two other years (Figure 6). The infiltration of meltwater into soils at temperatures below the freezing point of bulk water results in refreezing and the immediate release of latent heat (Kane et al., 2001). This process results in rapid warming of the soil to 0°C, after which soil temperatures stay constant at 0°C. At e.g. 10 cm this condition may persist for an extended period of time (Rennert et al., 2009, Figure 5). During this period (the

so called "zero curtain period"), the soil and permafrost below are effectively isolated from temperature variation. The thermal soil properties are strongly dependent on water content. At the plot level, sub-surface soil temperature was strongly negatively related to soil moisture (r = -0.76 [-0.85:-0.63]). This relationship can be explained by higher temperatures promoting the evaporation and drainage of water from soils, while wetter soils require more energy to warm up than dry soils, in particular with presence of underlying permafrost (Williams & Smith, 1989). This especially applies to organic soils overlying mineral soils. Because organic soils are porous and have relatively high hydraulic conductivities, they are very responsive to vertical infiltration and downslope water movement (Kane et al., 2001). This can result in rapid changes in the temperature at the organic–mineral soil interface at 2 and 5 cm depth. However, the thermal properties of these organic soils are highly dependent on moisture content. When dry, they form an effective insulator; when wet, an effective conductor.

Open Top Chambers (OTCs) increased the average air and sub-surface soil temperature. The air temperature increased by 0.7 ± 0.5 °C in 2016, 0.8 ± 0.8 °C in 2017 and 0.7 ± 0.7 °C in 2018 (June – September, measured with Hobo loggers; see Hendel, 2019). The soil sub-surface temperature increased by 0.8 ± 0.2 and 0.6 ± 0.2 °C in warming and the combined warming-icing treatments (mid-May – mid-September), however the warming effect was the strongest around peak growing season (in mid-July, Figure 4B). The warming effect of air temperature inside OTCs were comparable to the mean temperature increase from ITEX sites distributed across the Arctic (Bokhorst et al., 2013). Bokhorst et al. (2013) further found that while OTCs only marginally increase mean temperature, they have a larger influence on cumulative degree days and high-temperature extremes. Surprisingly, plant growth responses to OTCs are weaker in the high Arctic than in the low Arctic, probably because of lower irradiance close to the pole (Bokhorst et al., 2013). Exceptions to this occur in evergreen shrubs like *Dryas octopetala* (Elmendorf et al., 2012), which rarely occurred in our sites.

Plants' tissue temperature determines the activation of growth hormones (Sundberg et al., 2000). In our experiment, roots of vascular plants run deep in the active layers, easily down to 20 cm for the dwarf shrub *S. polaris*. The latter species compose the highest proportion of above ground biomass in our community, and correlates most strongly with NDVI measurements (Hendel, 2019). We therefore expect that the observed delay in spring-summer soil temperature increase caused by icing, and the increase of summer temperature by OTCs, can alter patterns of primary production across the growing season.
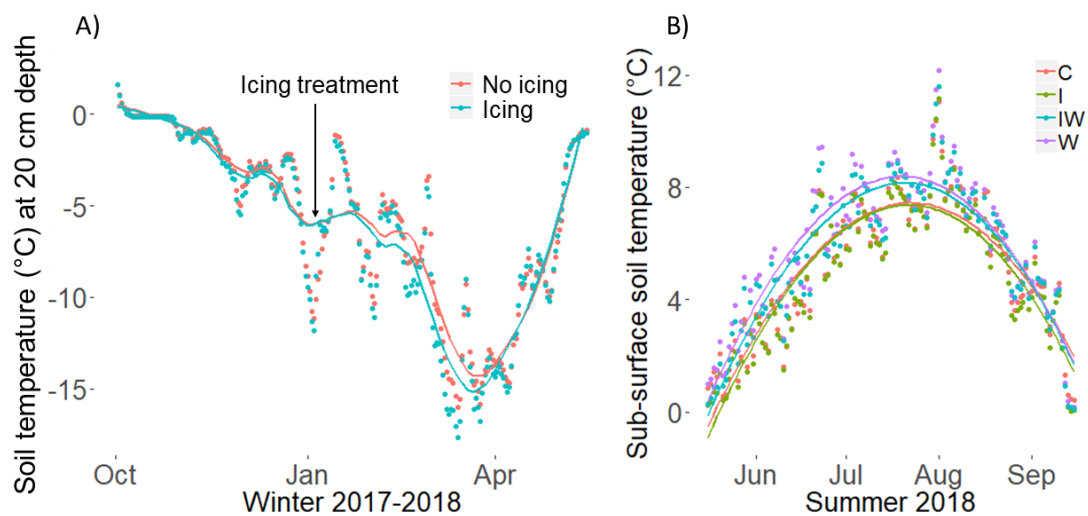

Figure 4 Soil temperature in A) winter 2017/2018 at 20 cm depth, averaged over 18 plots (6 per blocks) and B) summer 2018 at the sub-surface (2 cm depth, below the moss layer) averaged over 36 plots (12 per blocks). Points indicate the daily average raw data and the smoothed curves are plotted with their standard error. The date of the icing treatment is indicated by the black arrow.
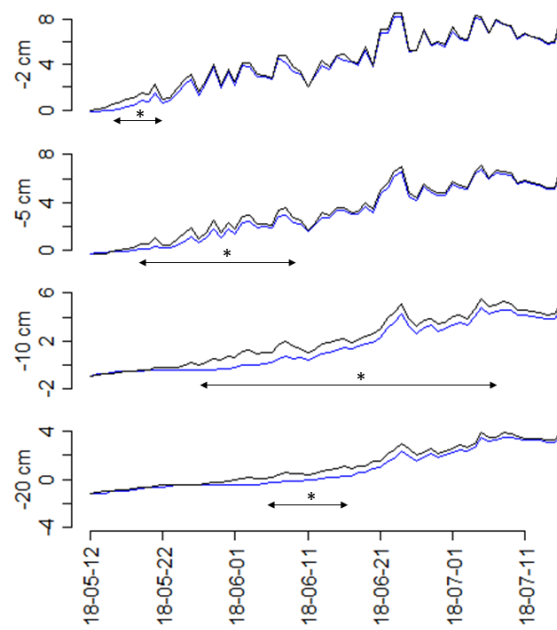
Figure 5 Soil temperature at different depth around snowmelt (6-12 loggers in each of the three blocks) extracted from linear-mixed effect models accounting for plots within blocks and daily replication. The blue line corresponds to icing plots and the black line to control plots. The horizontal arrows show the period of consecutive significant difference between curves.
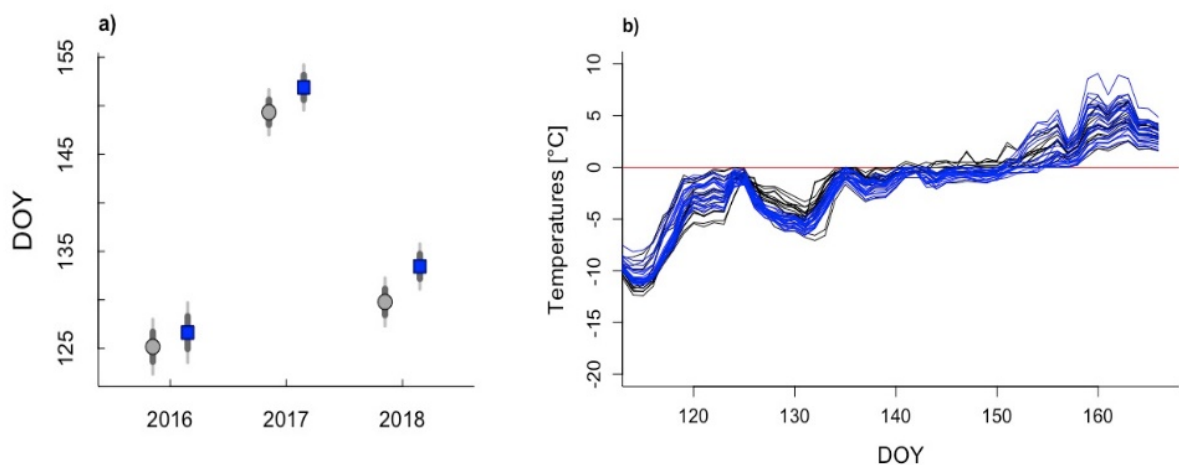
Figure 6 Time of snow/ice-melting in experimental plots. The timing was defined as the day of the year (DOY) when mean soil sub-surface temperatures (-2 cm) first exceeded 0°C. The estimates/values of the icing plots are represented in a blue color while the control plots are represented in grey/black. a) The estimated day of snow/ice-melt for control and icing plots across the years 2016 - 2018 based on linear mixed-effects models. b) The course of the soil surface temperatures in 2017 around the time of snow/ice-melt. The figure is reproduced from Hendel et al., (2019).

4.2   Community-level productivity

Plant growth is highly variable among years in Svalbard (Van der Wal & Stien, 2014, Le Moullec et al., 2018), reflecting the large fluctuations in high Arctic weather conditions. The NDVI, an index for primary production, has a typical bell shape across the growing season, delimitated by snow-melt and senescence. Relative to the extremely short growing season, timing of snow-melt is highly variable between years (Figure 6), in contrast to senescence drivers like light intensity, which can result in a compressed growing season in late snow-melt years (Cooper et al., 2011). The inflection point of the NDVI curve marks the peak growing season (Figure 7). The NDVI curve bell shape can change amplitude and can be more or less skewed, advancing or delaying the day of the peak growing season, which in turns changes the cumulative biomass produced before and after the peak growing season (Figure 7). For example, in 2018 (Figure 7), there was higher primary production in the icing x warming interaction treatment than in

control plots (i.e. higher amplitude), while the icing treatment only delayed the day of the peak growing season. Nonetheless, the overall result may indicate that cumulative biomass produced across an entire field season was not influenced by our treatments (Fig. 8A). However, the timing of when biomass was produced was delayed with icing (Fig. 8B and C). There was significantly reduced cumulated primary production in the first phase of the growing season, but a compensating increase in the second phase. As winter warm spells with above-zero temperatures are becoming more frequent, one arising question is how this will affect the ecosystem. As studies in the context of increasing summer temperatures have shown, a shift in the timing of primary production can change phenology patterns and ecosystem functioning, affecting the timing of resource availability for herbivores (Post & Forchhammer, 2008) and soil dynamics, including carbon fluxes (Welker et al., 2000, Leffler et al., 2016).

Thus, while previous pilot studies found physiological damage on plants and decaying plant material, possibly contributing to "Arctic browning" (Milner et al., 2016, Phoenix & Bjerke, 2016; Bjerke et al., 2017), we found a shift in the growing season. The amplitude of maximum NDVI was surprisingly constant across years and treatments. One clear exception occurred in 2017, when maximum NDVI in plots exposed to the icing treatment (icing and icing x warming) greatly overshot control and warming plots. This happened along with an extreme delay in the snow-melt as well as delayed date of the peak growing season, which was general across treatments. In fact, in 2017, the peak growing season was 12 days later (Figure 9), and the snow-melt 20 days later than any of the other years. The previous winter was characterized by heavy natural rain-on-snow events, encapsulating most plots in natural basal ice. Despite this, icing treatments (in addition to natural icing) significantly delayed the peak growing season by an average rate of 3.2 ± 1.4 days (Figure 9). Surprisingly, in the two very contrasting springs 2018 and 2019, in terms of spring-onset and air/soil temperature, the day of maximum primary production was similar. Hence, the spring onset of 2018 was early, but temperatures stayed low the entire June, while in 2019 the snow-melt was late, but June temperatures were high. This resulted in 41 ± 2 days from spring-onset to

peak growing season in 2018, compared to 34 ± 2 days in 2019. This illustrates the capacity of the plants in our study system to compress their growing season and thus increase growth rate in order to catch-up and compensate delays in spring-onset. This adaptive flexibility (plasticity) in responses to fluctuating environments probably explains the lack of treatment effects on the cumulative primary production across a field season (Figure 8A). This finds support in the resistance of plants' growth traits to icing in a laboratory experiment on two of the dominant vascular plants present in our experiments: *S. polaris* and *L. confusa*, although conducted on seedlings (Bjerke et al., 2018).
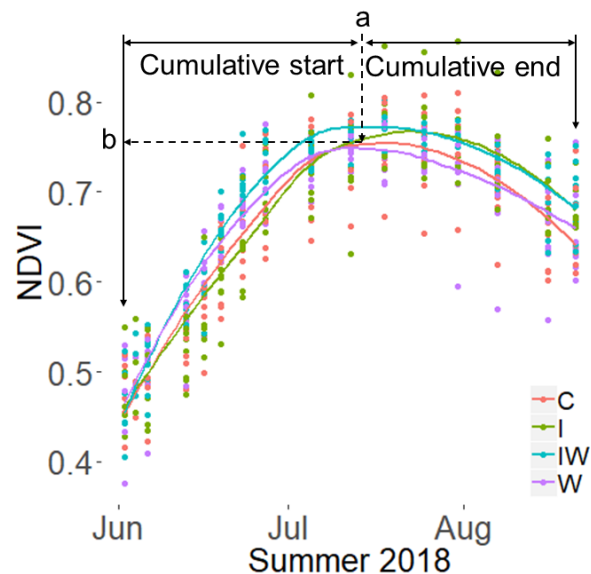

Figure 7 Example curve of NDVI measurements over summer 2018 (raw data averaged per treatment). The different metrics annotated on the graphs are further used for statistical analyses across treatments and years where a = day of year with maximum NDVI and b = value of maximum NDVI for the control plots. The cumulative start corresponds to the area below the curve from the first day of measurements to the day where control plots reach on average the maximum NDVI values (here represented as "a"). Similarly, the cumulative end corresponds to the area below the curve from the day where control plots reach on average the maximum NDVI values (here represented as "a") to the last day of measurements.
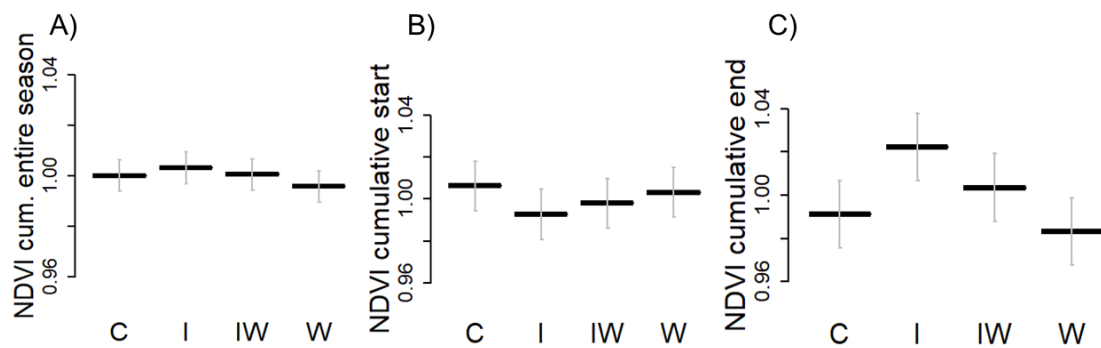
Figure 8 Cumulative NDVI curves A) for the entire field season i.e., from first to last day of measurements, B) for the first part of the summer, i.e. from the start of measurements to peak growing season, and C) for the second part of the summer, i.e. from peak growing season to end of measurements. The peak growing season day is defined as the day when control plots reach on average the maximum NDVI value. Estimates calculations are from GAM curves at the plot level over 2016-2019, and estimates are from linear-mixed effect models accounting for plots within blocks and yearly replication.
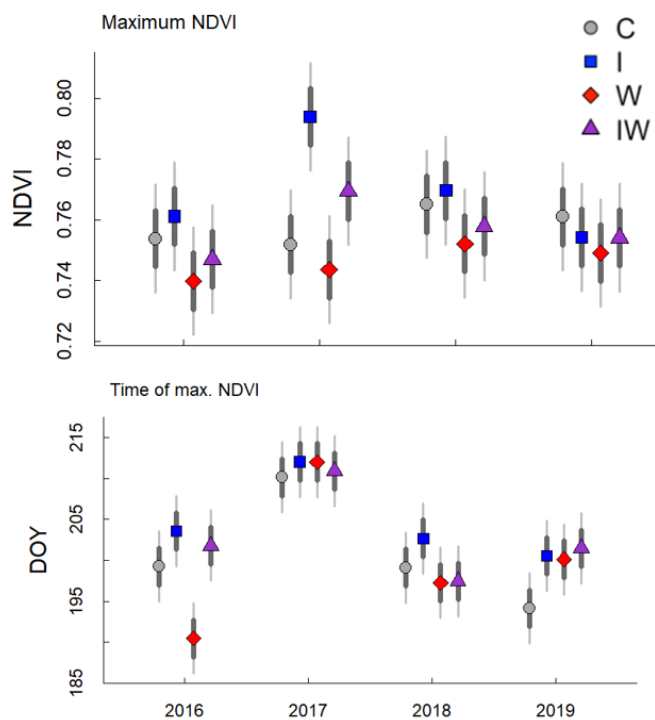
Figure 9 Variation in Normalized Difference Vegetation Index (NDVI) metrics across years and treatments. Upper panel: Maximum NDVI estimated. Lower panel: the day of year (DOY) of maximum NDVI. These metrics were calculated with GAM curves modelled at the plot level, then averaged with linear mixed effect models, as in Hendel (2019).

4.3   Flower production

As a result of a delayed growing season, a rapid plant development ("catch-up" effect) can be expected to have negative consequences for the reproduction of the plant. This was supported by our observations, which showed that the number of flowers in this mesic community was significantly reduced by about one third under icing treatment (Figure 10). A record low number of flowers after the extreme warm spells in 2012 was also documented nearby our experimental sites (Semenchuk et al., 2013). In these neighbouring communities dominated by the evergreen shrubs *D. octopetala* and *C. tetragona*, and the dwarf shrub *S. polaris* (in heath and mesic meadow habitats), an experimental manipulation of snow depth (and, thereby, length of snow-covered season) delayed the snow-melt by 6-12 days (compared to our ~3 days delay). This compressed

growing season also resulted in fewer flowers produced in most studied species (Cooper et al., 2011, Semenchuk et al., 2013). We did not include summer 2017 in the analysis of flower counts because (1) extreme winter events had covered most plots with basal ice, (2) snow-melt was extremely late, and (3) very few flowers were produced across treatments (10 ± 4 flowers per plot). Contrarily, summers 2018 and 2019 had consistent flowering responses to icing. Summer 2016 could not be included as the monitoring happened too late, i.e. after *S. polaris* male flowers senesced.

Milner et al. (2016) demonstrated a trade-off between energy allocation to plant growth instead of reproduction under experimental icing, however, the underlying mechanics may differ from our results. The evergreen shrub they studied, *C. tetragona*, suffered from direct icing effects causing mortality of shoots' apical buds, compensating growth of surviving secondary shoots, and reduced flowering. In our experiment, no obvious signs of mortality occurred (based on qualitative observations and species biomass measurements across treatments, results not shown here). A characteristic of evergreen shrubs is that they keep vital tissues above-ground in winter. On Svalbard, they mainly occur in habitats with deep snow protection. On the contrary, the deciduous shrub *S. polaris*, growing in a wide diversity of habitats, has most of its structure below-ground in winter (including shoots nested into the ground and roots; Le Moullec et al., 2019). The main mechanisms of icing effects therefore appear to occur indirectly, through soil processes in spring-summer.

The potential trade-off in energy allocation between growth and reproduction, as demonstrated here in response to icing, may in the long-term have evolutionary consequences (Franco & Silvertown, 1997). Nonetheless, the consequences for the dominant shrub in our community, *S. polaris*, are likely limited, as their seed viability was found to be robust to a compressed growing season (Cooper et al., 2011), and effects of an icing treatment in the lab were only minor (Bjerke et al., 2018).
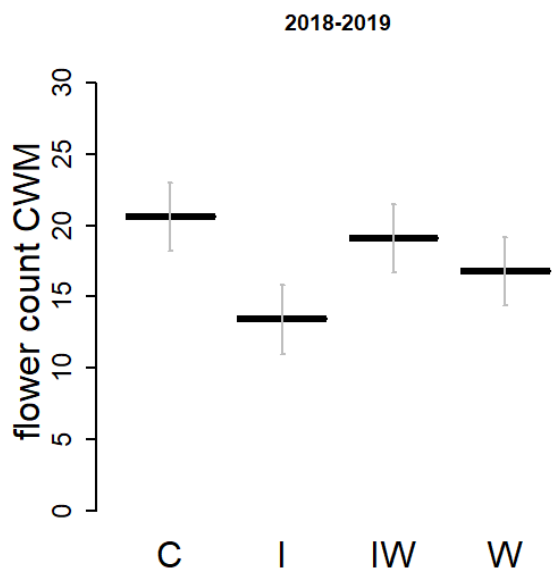
Figure 10 The community weighted mean of flower counts across the summers 2018 and 2019.

5 Conclusions and future prospects

This four-year field experiment in Svalbard suggests that heavy-rain-on-snow and basal icing in winter may strongly impact seasonal patterns of development of the soil-plant system in mesic tundra communities. The seasonal delay in community-level growth and productivity is probably a result of processes occurring in plant roots, as we found a significant delay in the thawing and spring-summer temperature rise in the soil due to the icing treatment. In terms of accumulated productivity over the summer, iced plots compensated (and in one year strongly overcompensated) for the delay effect from around the peak of the growing season, apparently at the cost of reduced flowering. Although the effect of natural annual variation was, for most variables, larger than the treatment effects, these documented impacts of icing on the plant community are far from negligible. They may also have wider ecosystem consequences, given the projected increase in rain-on-snow events. Importantly, icing treatment effects were also generally stronger than summer warming treatment effects. On the other hand, the plants growing in this mesic community – where icing occurs naturally now and then – seem overall rather adapted to the stress caused by such environmental perturbations. This is in contrast to species growing in other habitats, such as evergreen shrubs, which in a previous pilot study showed icing effects on both mortality, growth and reproduction. The results therefore underline the role of species- and community-specific adaptive plasticity in such a stochastic environment, especially under global warming. This advocates for future larger-scale studies of plant and soil responses to rain-on-snow and icing across plant functional types, vegetation communities and different regions of the Arctic.

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