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# Effects of Experimental Winter Warming on Trade-offs Between Growth and Reproduction in High Arctic shrubs

Master's thesis in Biology (Ecology, Behaviour, Evolution and Biosystematics)

Supervisor: Brage Bremset Hansen

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Faculty of Natural Sciences

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Kunnskap for en bedre verden





## Abstract

The Arctic is warming faster than the global average, and the frequency of extreme weather events in winter accelerates. Basal icing (i.e., ice on the ground) and thaw-freeze events (i.e., thawing and subsequent freezing) are two possible outcomes of episodic extreme winter warming and rain-on-snow events. Warm spells and rain-on-snow may encapsulate vegetation in basal ice or expose the vegetation to freezing temperatures due to melting of the insulating snowpack. Based on a common garden experiment in the high Arctic Svalbard, I investigated and compared the impact of basal ice on vegetative and reproductive variables in two contrasting shrub species, *Salix polaris* and *Cassiope tetragona*, and the trade-offs between these variables. In *S. polaris*, I also assessed the effects of thaw-freezing. Simulated heavy rain-on-snow events encased vegetation plots in basal ice, while electrical heaters were used to simulate thaw-freeze events in other plots. My results show that basal ice slightly elongated shoot growth increment and decreased the number of flowers of *S. polaris*, compared to controls, though it did not affect shoot survival. In *C. tetragona*, basal ice caused a strong decrease in shoot survival, including the survival of newly initiated juvenile side-shoots. This masked the effect on shoot initiation and compensatory growth of damaged *C. tetragona* shoots. In comparison, the thaw-freeze treatment of *S. polaris* clearly elongated shoot growth increment and decreased number of flowers to a higher degree than basal ice. Despite the impact of treatment on specific traits, I found no evidence that treatment mediated trade-offs between vegetative growth and reproduction, i.e., shoot growth and flower numbers in *S. polaris*, and proportion of alive shoots and flower numbers in *C. tetragona*. According to these experimental results, *S. polaris* may be less impacted by current and future increase in icing due to rain on snow events than *C. tetragona*. This may be due to differences in habitat and snow insulation requirements, along with life contrasting history traits and growth forms. Furthermore, in *S. polaris*, thaw-freeze events seem to have stronger impacts than icing, possibly by triggering de-acclimatization in the buds, leaving the buds less protected when frost returns. These experimental results add novel and nuanced insights into the variation in vegetation responses to high Arctic winter warming events and indicate that the effects of such events will depend on how they change the snow-pack properties.



## Sammendrag

Arktis varmes fortere enn det globale gjennomsnittet, og frekvensen av ekstremvær om vinteren øker. Bakkeis og tine-fryse episoder er to mulige utfall av ekstreme varmeperioder på vinteren og vinterregn. Disse kan dekke vegetasjonen i bakkeis eller eksponere vegetasjonen for svært lave temperaturer grunnet smelting av det isolerende snødekket. Basert på et 'common garden' eksperiment i det høyarktiske Svalbard undersøkte jeg og sammenlignet påvirkninger av bakkeis og tine-fryse episoder på vegetative og reproduktive variabler i *Salix polaris* og *Cassiope tetragona*, samt tildeling av ressurser mellom disse variablene. I *S. polaris* testet jeg også responsen av tine-fryse episoder. Bakkeis dannet av vinterregn var simulert ved å dekke vegetasjonen med is, mens elektriske ovner var brukt for å simulere tine-fryse episoder. Resultatene mine viser at bakkeis øker lengden på årlig skuddvekst til en viss grad i forhold til kontrollplantene. Disse i motsetning gikk ned i vekst etter de ble transplantert til hagen. I tillegg gikk antall blomster ned i forbindelse med bakkeis, selv om is ikke påvirker en annen proxy på reproduksjon. I *C. tetragona*, forårsaket bakkeis en sterk nedgang i overlevelse av skudd, deriblant også unge skudd og forsøk på kompensere vekst. I *S. polaris* økte lengden på årlig skuddvekst mer etter Tine-fryse episoder enn bakkeis. Antall blomster gikk også enda mer ned. Selv med disse innflytelsene på individuelle variabler, fant jeg ingen bevis på at bakkeis og tine-fryseperioder har endret tildelingen av ressurser mellom skuddvekst og blomsternummer i *S. polaris* eller mellom andel levende skudd og blomsternummer i *C. tetragona*. I henhold til disse eksperimentelle resultatene, kan det virke som om *S. polaris* vil bli mindre påvirket av en fremtid med mer vinterregn i forhold til *C. tetragona*. En grunn til denne forskjellen kan være deres ulike livshistorietrekk og vekstform. For eksempel gror *S. polaris* for det meste under moselaget, mens *C. tetragona* eksponerer større deler av biomassen sin over bakken, noe som gjør den mer utsatt for skade om vinteren. I *S. polaris*, tine-fryse episoder ser ut til å ha sterkere innvirkning enn bakkeis. Sannsynligvis utløser tining av-akklimatisering av skuddene, noe som gjør dem mindre beskyttet når frosten kommer tilbake. Disse resultatene gir en ny innsikt i vegetasjonsrespons til høyarktiske episoder av ekstrem vintervarming og indikerer at effekten av slike hendelser er knyttet til hvordan egenskapene til snødekket blir endret.





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## 1 Introduction

The Arctic region is warming twice as fast as the global average through Arctic amplification (Cohen et al., 2014, Screen and Simmonds, 2010). Majority of the warming occurs during the winter, with a heightened frequency of episodic warm spells and extreme weather (Graham et al., 2017, Walsh et al., 2020). Across the Arctic more precipitation is falling as rain instead of snow during winter (Bintanja and Andry, 2017). Winter warming can paradoxically lead to higher risk of damage on the vegetation, as the ground can be covered in basal ice following a rain-on-snow event (ROS) (Peeters et al., 2019) or stand bare following a thaw-freeze event mid-winter (Bokhorst et al., 2011). This stands in contrast to the increase in 'greenness' observed the last decades (Piao et al., 2020).

The Arctic is greening through higher biomass productivity and shrub expansion (Frost et al., 2021), with increasing temperature being one of the main drivers (Raynolds et al., 2008, Vickers et al., 2016). The vegetation is generally sensitive to warming but can give heterogeneous and unpredictable responses (Bintanja and Selten, 2014, Vihma, 2014). In the last years the greening trend has de-accelerated and in some cases even reversed (Vickers et al., 2016). Arctic browning describes this trend of lowered correlation between summer warming and vegetation productivity, and we can expect other drivers behind this phenomenon such as damage during winter and extreme weather (Phoenix and Bjerke, 2016, Bjerke et al., 2014), along with nutrient limitation (Huang et al., 2017). Flowering also shows a similar diminishing response to warming with high yearly variation (Kremers et al., 2015). These two opposing trends are creating complexities that is difficult to entangle, and makes the prediction of community response to climate change challenging (Phoenix and Treharne, 2022). The increasing frequency of extreme events during winter can oppose the higher productivity during summer warming, which may lead to a higher level of heterogeneity in the landscape locally (Bjerke et al., 2017) and globally (Frost et al., 2021).

Arctic warming is not spatiotemporally uniform, and in some areas is strongest in autumn and winter (Cohen et al., 2014). The predicted increase of ROS is mainly due to accelerated local evaporation enabled and lack of albedo by sea ice retreat (Bintanja and Selten, 2014, Vihma, 2014). In addition, warm and moist air enters the Arctic from lower latitudes in short but intense episodes during autumn and winter (Woods and Caballero, 2016). These warm anomalies contributes to the observed heating along with diabatic heating such as friction, solar and terrestrial radiation (Papritz, 2020). In the last 20 years, warming periods have become more frequent and intense (Pedersen et al., 2015). They predict that the current warming trend will continue, and that Arctic areas such as Svalbard will see a threefold increase of warm winters in the next 50-100 years, compared to the period between 1985-2014.

Winter warming and ROS may cause two phenomena called basal ice (also called "ground ice" or "icing") and thaw-freeze events (Bokhorst et al., 2011). Basal ice normally forms by rain permeating the snow to pool at the soil surface. The pooled water release latent heat as it freezes, raising the soil temperature to near 0°C (Putkonen and Roe, 2003). This may only last for a few days before the soil temperature is back to near regular regime (Le Moullec et al., 2019). Basal ice can also form by the liquid water released from the snowpack during a warm spell, even if ROS did not occur (Rennert et al., 2009) or snow freezing on unfrozen soil (Rasmus et al., 2018). The thickness of the ice layer varies, and while the median may lie anywhere between ~5 cm and ~20 cm at some sites, thickness over 40 cm has been observed (Peeters et al., 2019). The ice may encase vegetation completely (Bjerke et al., 2017), and make it unavailable for herbivores such as reindeer or musk ox to access (Hansen et al., 2011, Putkonen et al., 2009). Being encased in ice may cause hypoxia and anoxia in the plant as respiratory gases cannot penetrate though, or physical damage to the plant cell as it freezes (Andews, 1996).

Thaw-freeze events are defined as episodic warming periods during winter, where the snow melts and expose the vegetation to the returning freezing temperatures (Bokhorst et al., 2008). This increased risk of frost damage stands as a paradox to the increasing winter temperatures (Gu et al., 2008). This has shown to be considerable damaging to Arctic vegetation, with well-documented examples in the in sub-arctic heathland (Bokhorst et al., 2011, Bokhorst et al., 2012, Bokhorst et al., 2009). During the thawing period, the plants de-acclimatise as it initiate the end of dormancy (Rapacz, 2002). This makes them less equipped to withstand freezing temperatures (Bokhorst et al., 2010). This can lead to damage or death of both leaf and flower buds. Overwintering flower buds have shown to be especially sensitive, as they balance between the reward of longer growing season and the risk of frost mortality in the face of advanced spring onset (Inouye, 2008).

Much of the previous research on the effect winter warming has on vegetation is focused on snow depth and timing of melting (Cooper, 2014, Mallik et al., 2011, Khorsand Rosa et al., 2015). Less has been done on the effect of ROS and basal ice on vascular plants.

However, Milner et al. (2016) found that basal ice increased shoot mortality and damaged shoots in *Cassiope tetragona*. Clustered below the dead or damaged apical tips were new green juvenile side shoots. Additionally, flowering decreased after icing, prompting a question of trade-offs between shoot growth and reproduction. Le Moullec et al. (2019) applied a similar icing experiment on a different community dominated by *S. polaris* at Svalbard. They found that the timing of biomass production was delayed with icing, but the plants caught up later in the growing season, so the cumulative effects of treatment across the summer were not visible. However, the catch-up had influences on flower

production, as number of flowers in this mesic community was significantly reduced in the icing treatment in the second year of treatment.

While Le Moullec et al. (2019) found delayed phenology, Milner et al. (2016) found physiological damage. Mortality was not observed in the first mentioned study, and therefore the underlying mechanism behind the observed trade-off may differ. Le Moullec et al. (2019) did not observe damage on mature *S. polaris*, but seedlings have been observed to show damage with following compensatory growth after experiencing basal ice (Bjerke et al., 2018). These contrasting responses may be related to the different life history traits of *S. polaris* and *C. tetragona*. While *C. tetragona* is an evergreen shrub with most of its biomass above ground, *S. polaris* is a deciduous shrub with who have most of its biomass within the moss layer (Myers-Smith et al., 2015, Havstrom et al., 1995).

Plants in the Arctic have a limited resources (Shaver et al., 2001, Chapin, 1983). Reproduction is costly, and flower production takes resources from vegetative traits related to vegetative growth or herbivory defence (Obeso, 2002). Trade-off is defined as a negative relationship between reproductive and vegetative traits (Reznick, 1985). How plants allocate their resources are dependent and constrained by their dominant growth strategy, environmental conditions, and evolutionary history and plasticity (Maessen et al., 1983, Obeso, 2002). Little study has been done on trade-offs in the Arctic, but it has been explored in mid-latitude and alpine regions (Bajcz and Drummond, 2017, Hautier et al., 2009, Jongejans et al., 2006).

Arctic plants tend to favour asexual reproduction through vegetative propagation. This may be linked to limited seedbanks or failure to germinate. This is the case for *S. polaris* and *C. tetragona* (Cooper et al., 2004). The predicted temperature increase during summer may shift this strategy towards sexual reproduction (Klady et al., 2011), as warmer ground temperatures seem to enhance seed biomass and germination. Basal ice and thaw-freeze events may disrupt this trend, as winter extreme events may damage the reproductive effort (i.e. flower buds) given in the previous summer and affect the allocation between reproductive and vegetative structures.

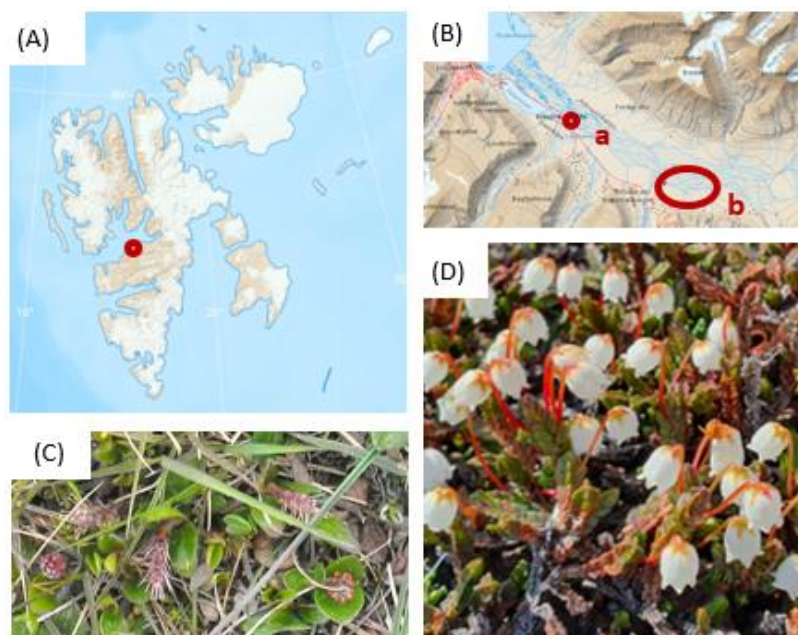
The purpose of this study was to further understand the impact of warmer and wetter winters on Arctic shrubs, by experimentally investigating effects of basal ice and thaw-freeze treatments on vegetative and reproductive traits, and trade-offs between them, in *S. polaris* and *C. tetragona* on Svalbard. This was done in a common garden experiment. I expected to see higher shoot mortality followed by an increase in growth as compensation. Along with a decrease in energy allocated to reproduction and thereby different trade-off between growth and reproduction in relation to treatments. However, where *C. tetragona* might show strong responses as observed in Milner et al. (2016), *S. polaris* may respond to a lower degree after basal ice (Le Moullec et al., 2019). Though little is known regarding the effect of basal ice on vegetation in the high-Arctic, even less is known about effects of thaw-freeze. Based on the observations of Bokhorst et al. (2011), I expected thaw freeze to give a elicit a greater response than basal ice. By conducting the experiment in a common garden, I will be able to distinguish treatment response from other abiotic factors as both treatment and control plots experience the same environment. Common gardens have been used extensively in genetic studies in both plants and other taxa (de Villemerueil et al., 2016), and has great potential to bridge levels of biological organisation and disciplines (Huxman et al., 2021).

## 2 Methodology

### 2.1 Study site and species

A common garden experiment was established in 2018, about 4 km outside of Longyearbyen in Adventdalen, Svalbard (Fig. 1B(a)). The archipelago is characterized by wide gradients of temperatures and precipitations, and the increase in temperature and precipitation is most pronounced in the southern and central parts (van Pelt et al., 2019). Warming of 3-5°C has been seen from 1971 to 2017, with it being more pronounced in the winter compared to the summer (Hanssen-Bauer et al., 2019). The mean observed surface temperature at the experimental site from start to finish of the study was  $-3.7 \pm 9$  °C and the mean daily precipitation was  $0.3 \pm 0.8$  mm (at Adventdalen weather station, Norwegian Meteorological Institute).

The growing season is short, with high spatiotemporal variability of spring onset (Karlsen et al., 2014). The region regularly experiences ROS events, and they are more frequent in the southwest (van Pelt et al., 2016, Wickström et al., 2020). Before 1998, basal ice caused by ROS happened on average every four years, but ever since there is rarely a year that goes by without basal ice formation (Peeters et al., 2019). These events have shown to be catastrophic to the herbivore community, with starvation-induced mortality in reindeers (Hansen et al., 2014) and in the invertebrate community (Coulson et al., 2000).



**Figure 1** (A) map over Svalbard, the red dot indicate Adventdalen (Polarinstitutt, 2022b). (B) a ( $78.20240^{\circ}\text{N}$ ,  $15.82931^{\circ}\text{E}$ ) is the site of our common garden in Adventdalen and b ( $78.17413^{\circ}\text{N}$ ,  $16.02156^{\circ}\text{E}$ ) is the location of the in-situ site (Polarinstitutt, 2022a). (C) is a picture of male *S. polaris* taken by me and (D) is a picture of *C. tetragona* also taken by me.

The two principal species in this study are the woody shrubs polar willow *Salix polaris* (Fig. 1C) and Arctic bell heather *Cassiope tetragona* (Fig. 1D). *S. polaris* is a deciduous shrub with most of its biomass below the moss layer. It is protected by soil and moss with only the tip with a few leaves and reproductive structures are peeking above-ground during summer (Dormann et al., 2004, Gjærevoll, 1999). *C. tetragona* on the other hand, is evergreen with most of its biomass above-ground (Eidesen et al., 2007) and form their flower buds the previous year (Semenchuk et al., 2013). *S. polaris* is a late successional plant that reproduce mainly vegetatively through stolons, though they also sexual reproduce through seed production (Nakatsubo et al., 2010). Germination is limited in the field for both species and they often struggle to establish through seed dispersal alone (Cooper et al., 2004, Nakatsubo et al., 2010).

During the winter, *C. tetragona* relies on snow for protection against the harsh environmental conditions (Blok et al., 2015), while *S. polaris* often get sufficient protection from the soil and therefore can grow in more exposed environments. Though both species grows in snowbeds, we often see *C. tetragona* along depressions and in drainage channels (Bjerke et al., 2017). On a landscape scale in the Arctic, different species of dominance are often layered along a gradient of incline and soil water content (Elberling et al., 2008). In other areas, *S. polaris* and *C. tetragona* together with the rest of the community form a heterogenic mosaic of microhabitats, which was also observed at the in-situ location. It is worth noting that both species survive within a large environmental gradient, and have been observed within a range of conditions (Margorie and Freedman, 1987)

## 2.2 Experimental design

In the summer of 2018, 54 plots from mesic and wet habitats were transplanted to the common garden by Aurora station from the in-situ control site in Adventdalen, about 5 km further in the valley (Fig. 1 B(b)). The selected plots all consisted of *S. polaris* and contain a diverse plant community. The wet habitats had a moss layer of  $8 \pm 2$  cm, while mesic had a  $3 \pm 1$  cm moss layer.

21 plots were transported from a wet community, while 33 were from a mesic community. The transplants were collected in a 100-meter radius and extracted between 26.07-03.08.2018. Turves of 19.5 cm diameter wide and 20 cm deep were cut, extracted, and placed in pipes, which function as bottomless pots. Gravel and sand from the riverbed were used as filling between each pot after being transplanted to the garden (Fig. 2A). After transplanting, all the plots were watered twice (mesic:  $2 \times 0.5$  L, wet:  $2 \times 1$  L).

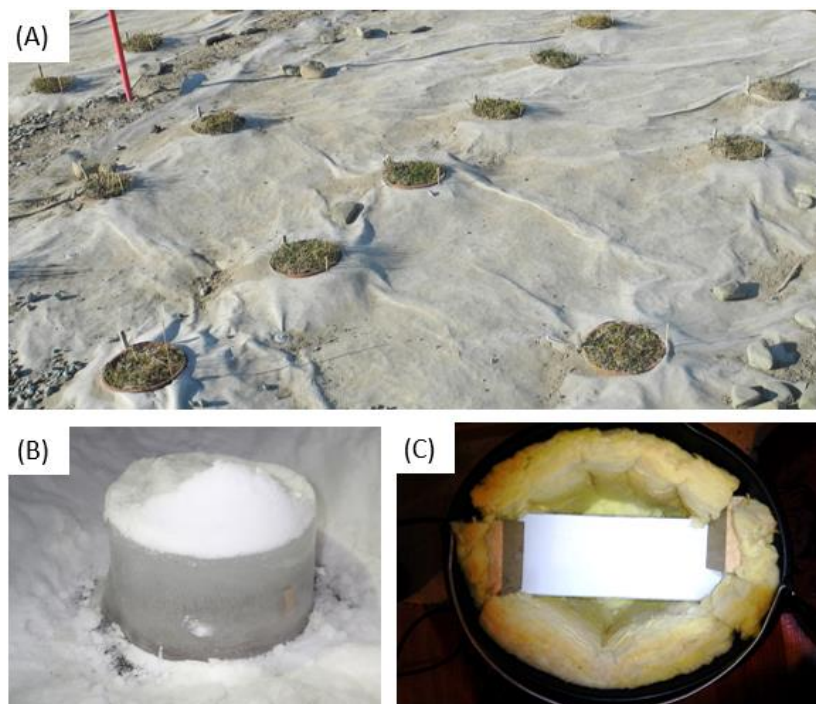
Once the plots were placed in the garden they were randomly allocated a treatment of basal icing ( $n=22$ ) and thaw-freeze ( $n=15$ ) and placed at random with at least 40 cm between each plot. In addition, there are control plots in the garden ( $n=37$ , in 2019 and



n=23 in 2020) and *in-situ* (n=32) (Table A1, Appendix). Of the *in-situ* plots, ten pairs are of the mesic community and six pairs of the wet community. In each pair, one plot is in a pot to test for the “pot-effect”, while the other one is undisturbed to have a true control.

In the summer of 2019, 12 plots dominated by *Cassiope tetragona* were added. Of these plots, six were given icing treatments while six acted as control. In Adventdalen, five plot pairs remain as *in-situ* controls, one half in a pot (*in-situ* C-P), and the other half without any disturbance (*in-situ* C).

The icing treatment was initiated in February in 2019 and January in 2020 and 2021. To make the ice layer, a 30 cm diameter bottomless bucket were placed upside down above the plot. Ice and snow were mixed and poured into the bucket until about ~15 cm (Fig 2B). To prevent ice melt during the winter the bucket were kept until spring in 2020 and 2021. To avoid the controls getting a “treatment” of basal ice during natural ROS events, the weather was monitored, and a tarp expended on top of the plots in the garden in the event of rain. This only happened thrice, once during the winter of 2020/21 and twice during the winter of 2018/19.



**Figure 2** (A) Picture of a part of the garden during summer of 2021. The plots are placed at random with a sheet covering the gravel filling between the plots. Picture by me. (B) picture of the icing treatment during winter. Picture by Mathilde Le Moullec. (C) Picture of the insulated bucket with an electrical heater which is used to simulate thaw-freeze events. Picture by Mathilde Le Moullec.

For the thaw-freeze treatment, snow free plots were thawed by a frost guard electric heater (60 W) inside an insulated bucket in 2020 and 2021 (Fig. 2C). Temperature was monitored during treatment, and heating settings changed accordingly to accurately thaw the plots with an air temperature of 10 degrees on average. After six days of thawing, the heaters were removed, and the plots allowed to refreeze.

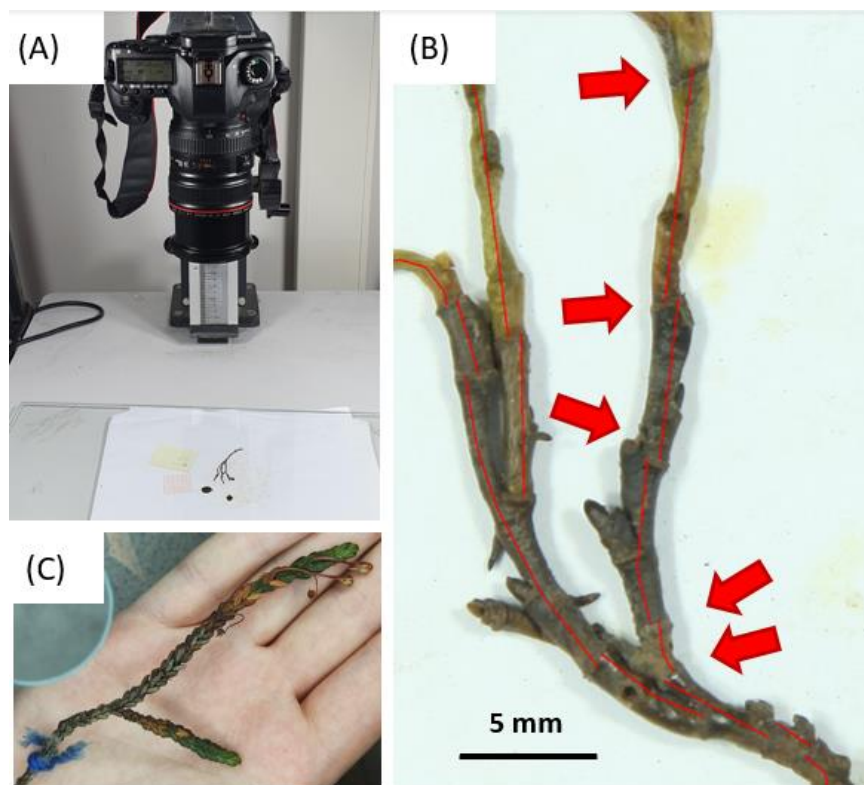
## 2.3 Shoot collection and measurements

### 2.3.1 *S. polaris* shoot increment

Radial dendrochronology of secondary growth in *S. polaris* highly correlates with temperature (Buchwal et al., 2013) and has been used as a proxy for past climate (Owczarek and Opała, 2016) Though some studies on the use of lateral dendrochronology between winter scars exist (Dormann and Skarpe, 2002, Myers-Smith et al., 2015), the potential of lateral dendrochronology has been less applied. To get a measure of yearly growth, I harvested *S. polaris* from the garden at the peak growing season in the end of July 2021. Increments of *S. polaris* may not be fully elongated before harvest, but this should be equal across treatments (unless treatment is changed phenological development of shoots). After excavating the plots, we retrieved individual shoots by separating the plot, without damaging the shoots. Sand and dirt were then washed off and the samples stored in a freezer of -18 °C.

To get readable shoots for my analysis, I decided on a protocol for requirements to follow during a preselection. (1) they need to have an apical tip, if the tip is broken off, we do not know which year each growth increment is from. (2) the shoot needs to be the length of at least 6 growth increments, three years during the experiment and three years before the transplant to act as controls. I made this preselection of at least 10 shoots per plot, if available. (3) avoid shoots with clear broken stems, as there may be a gap in shoot increment, i.e., the stem broke in 2017, but 3 years of growth broke off, leaving a gap between 2014 and the next growing season of 2018. (4) it needs to be possible to see the growth marks, some stems that has been exposed above the surface grow a thick layer of bark, leaving the rings difficult to read. While using these requirements, I choose the first suitable shoot that I found in each pile of *S. polaris*. No conscious bias related to number of side shoots, shoot thickness or other features has been implemented.

In the photo lab, I made a new selection of 5-6 shoots for pictures and measurement. I used a photography system where a DSLR camera was expended right above the sample, with the lens facing downward (Fig. 3A). The shoot sample was laid on top of white paper, with shoot ID and mm paper beside it for calibration. On top, a glass plate was laid to keep the shoot flat. At least one photo or more of each side was taken until all the side shoots are in focus. Afterwards, each picture was measured in Image J (Schneider et al., 2012). By using a segmented line, I traced the stem and measured the length between each winter scar while comparing to the actual sample to make sure I get all the winter scars correctly. During this process other variables such as death of shoot tips and year of shoot initiation was recorded (Fig. A1, appendix A).



**Figure 3** (A) The camera set-up for taking pictures of individual shoots. On the table is a *S. polaris* shoot, millimetre paper for scale and the shoot ID below a glass plate. (B) Picture of a *S. polaris* shoot after measurement. Arrows point to the winter scars. This side shoot has five increments, the top one being from 2021. (C) Sample of a marked *C. tetragona* with one side-shoot and two flowers from 2021 at the top and

### 2.3.2 *S. polaris* leaf and catkin biomass

After taking the picture of shoots (see section 2.3.1), the total biomass of leaves and catkins (the female inflorescence) (Fig. A1B, Appendix A) in each plot was separated. Catkins were counted per plot, along with the number of seed capsules per catkin. Then the catkins were washed and dried for two days at 60 °C. Afterwards, we weighted them to nearest 0.001 g.

For detailed description of separation of biomass and related measurements, see Røssum (2022).

### 2.3.3 *S. polaris* flower count

*S. polaris* have been counted yearly between 2019 to 2021. Male flowers senescence earlier than female flowers, and they fall of the stem when they do. To make sure we get the correct number of male flowers, we performed the flower count before they fall off around mid-July. A pipe frame (19.5 cm diameter) subdivided into four by a string was placed on the plot, encircling it (Fig. A2C, Appendix A) The frame was places at the same place every time and the count were done in the same order in each of the four sub-squares. I summed the four squares so from here on out the flower count is always on plot level.

### 2.3.4 Cassiope

During the addition of Cassiope to the experiment in the summer of 2019, we selected and marked alive apical shoots in each plot (n=5) at both the common garden experimental site and in-situ in Adventdalen. Then we surveyed whether the side shoots above the mark of each individual were alive or dead. To keep track of new shoots, we made a distinction between normal side shoots and "juvenile side shoots". These are <1cm long. These were also marked as alive or dead. This was repeated in 2020 in addition to recording whether the apical shoot was alive or dead. During this survey the total number of flowers per plot was counted.

In early August 2021, we sampled all the marked shoots after counting the total number of flowers in each plot. The shoots were stored in a freezer -18° Celsius. In a lab I performed the beforementioned survey again.

## 2.4 Statistical analysis

### 2.4.1 *Salix polaris*

To analyse the data, a variety of linear mixed effect models (LMM) from the 'lme4' package in R (Bates et al., 2015) were used, since this experimental design uses repeated sampling over several years. Common predictors are treatment (three level factor: icing [I], thaw-freeze [Th] and control [C]) and year (three-level factor: 2021, 2020, 2019). For plot level analysis the random intercept structure is plot ID, due to repeated measurements. I have tested both additive and interaction effects. Additive effects are defined as a fixed effect that are added to other predictor variables to evaluate its effect on the response variable. Interaction effect is defined as a variable that has a different effect on the response depending on the value of a third variable. Interaction terms have been tested to assess if the effect of the vegetative predictor differ with treatment, which is how I will determine trade-off. Models with and without interaction terms was compared using second-order Akaike Information Criterion (AIC<sub>c</sub>) by the 'MuMIn' package (Barton, 2020). If the interaction models have  $>\Delta 2$  AIC<sub>c</sub> units more compared to the additive models there is no evidence of trade-off.

*Timeline.* To see how the shoot growth within each treatment group has changed from 2016 to 2021, I made a timeline by adding an interaction term between year (six-level factor: 2021 – 2016) and treatment. The model is on individual increment level. Because there is large variation of increment length between shoots, increment is log transformed. Due to hierarchal sampling of increments within a shoot over several years per plot, random intercepts are included with the whole shoot ID nested within plot ID. Note that increments between 2016 and 2018 are in-situ and undisturbed by the experiment, while between 2019 and 2021 they have been transplanted to the garden and treatment has been initiated. These two groups will from now on be called "pre-treatment" and "post-treatment".

*Before and after treatment.* To test how the shoot growth increment has changed between pre-treatment and post-treatment, I used the "period" (two-level factor: pre-treatment and post-treatment) and treatment as interacting predictors of shoot increment. Here the random structure is shoot ID nested within plot ID, in addition to a random intercept of year (six-level factor: 2021 – 2016).

*Shoot growth.* To test the response of shoot growth increment to treatment in *S. polaris* I performed a LMM with treatment (I, Th and C) and year (2021 and 2020) as additive predictors of shoot growth increments (continuous). I also did a separate model, because thaw-freeze simulation is not performed in 2019, with treatment (I and C) and year (2021,

2020, 2019) as predictors. Random structure for both models is shoot ID nested within plot ID.

*Flower count.* I first tested the difference in flower number in each plot between treatments by using a generalized linear mixed effect model (GLMM) with treatment (I, Th and C) and year (2021 and 2020) as predictors. As there was sign of over dispersion I used a negative binomial distribution with log link. In addition, I tested icing effects in a separate model with treatment (I and C) and year (2021, 2020, 2019) to see effects of icing in 2019. The random intercept structure for both models is plot ID.

*Trade-off in flower number.* To test the possibility for trade-off between increment growth and flower count, I used a GLMM with the log of shoot increment (continuous), treatment (I, Th and C) and year (2021 and 2020) as the predictors of number of flowers. Plot ID was set as random intercept. As the response is count data with signs of overdispersion, I used a negative binomial distribution with log link. Because flower count is measured on plot level, I upscaled shoot increment by predicting the mean shoot increment in each plot per year with an LMM. The model had the same random structure as previous increment models.

*Leaf biomass.* I used a linear model (LM) with treatment (I, Th and C) as the predictor to test how the leaf weight in 2021 differ between treatments. As the leaf weight was right skewed, I used a square root transformation to obtain a normal distribution for the residuals.

*Catkin proxy.* The weight of catkins is strongly correlated to the number of catkins in the plot. To investigate how treatment influence this relation, I made a proxy by extracting the residuals of an LM with the number of catkins per plot (integer) as the predictor of weight of catkins per plot (continuous). I square rooted the weight to normalize the residuals. Positive values in the proxy indicate fewer, but heavier catkins. Negative values indicate more, but lighter catkins.

*Trade-off in proxy.* The catkin proxy was then the response variable in a LM with predictors of leaf weight (per plot, square rooted) and treatment (I, Th and C). To test for trade-off between the reproductive effort (proxy) and leaves, I compared the AIC<sub>c</sub> of the additive model to an interaction version of the model.

#### 2.4.2 *Cassiope tetragona*

For *C. tetragona*, all the data are counts, and GLMMs were used. The common predictors were treatment (four-level factor: icing [I] and control [C], in situ control [in-situ-C] and potted in situ control [in-situ-C\_P]) and year (three-level factor: 2021, 2020 and 2019). Random intercept structure is plot ID due to hierarchal sampling over several years.



*Apical shoots.* To test the treatment effect on the survival of apical shoots (two-level factor: yes, no), I used treatment (I, C, in-situ-C and in-situ-C\_P) and year (2020 and 2021) as additive predictors. 2019 was not included as all apical shoots were selected to be alive. The GLMM used a logit link function with binomial distribution.

*Side-shoot survival.* Treatment effect on side-shoot survival was tested in a binomial GLMM with the proportion of alive to dead shoots per individual as the response variable. Predictors were treatment (I, C, in-situ-C, and in-situ-C\_P) and year (2021, 2020 and 2019). To verify if the potential treatment effect changed between years, I added an interaction term between treatment and year.

*Juvenile side-shoots.* I tested if the effect of treatment on side-shoot survival changed with juvenile side-shoots. I did a similar analysis as above but changed the predictor to the proportion of alive to dead juvenile shoots. In addition, I tested treatment effect in the number of alive juvenile shoots (integer). Here I use a log link function with poisson distribution in the GLMM with treatment (I, C, in-situ-C, and in-situ-C\_P) and year (2021, 2020 and 2019) as predictors. To see whether the total count of juveniles side-shoots dead and alive differed between treatments, I used a similar model as above but with the total count as the response variable.

*Flower count.* I tested whether flower count differed between treatments and between the controls by using treatment (I, C, in-situ-C, and in-situ-C\_P) and year (2021 and 2020) as predictors. I used a log link function with poisson distribution and used the optimizer "bobyqa" due to convergence issues.

*Trade-off flower number.* To test whether treatment affected trade-off between number and flowers and the proportion of alive side shoots, I compared an additive- and interaction model with the same response and predictors by AIC<sub>c</sub>. The predictors were the proportion of alive to dead shoots and treatment (I and C). As there were signs of overdispersion, I used a negative binomial distribution with a log link function. Here I only used data from the common garden in 2020, because icing plots had no flowers in 2021.

All the estimates have been extracted and back transformed where appropriate. Log transformations are transformed back by their exponential, square roots by square and logit by inverse logit. Visualizations has been produced by the package 'ggplot2' (Wickham, 2016) and output tables have been produced by the 'sjPlot' package (Lüdecke, 2021).



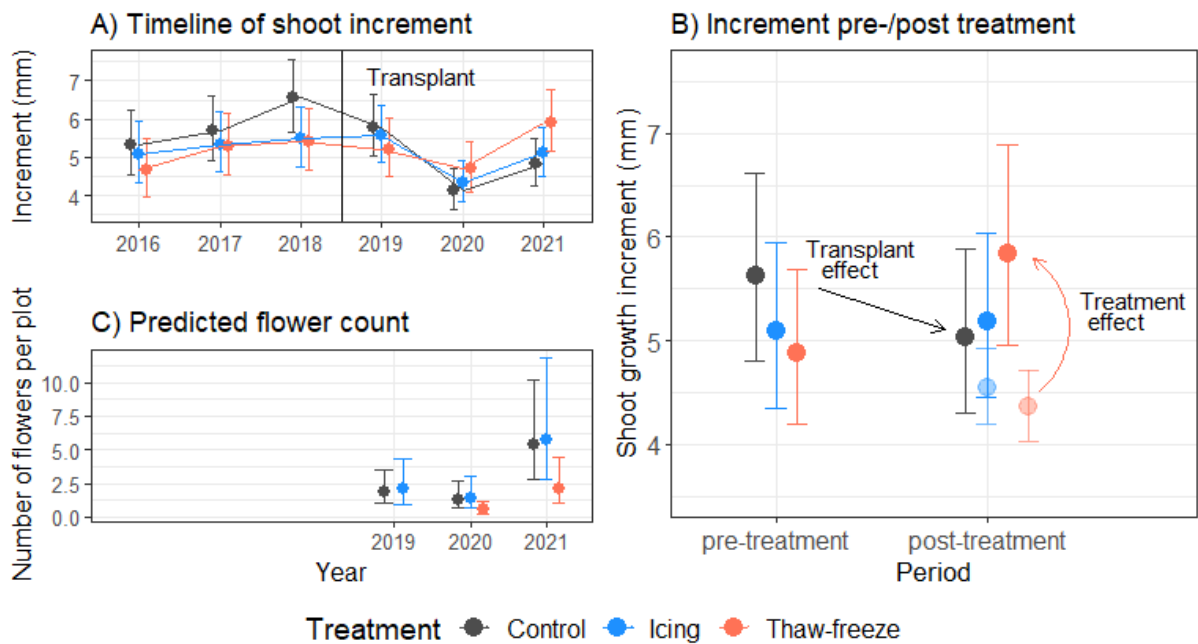
## 3 Results

### 3.1 Salix

#### 3.1.1 Yearly vegetative traits of *S. polaris*

The yearly mean growth stayed somewhat consistent the 3 years before treatment (5.1 mm [4.5 – 5.7]), predicted mean [95% confidence interval]) (Figure 4A). In the six-year period, the year with the highest increment growth was 2018 in the pre-treatment period (5.80 mm [5.34 – 6.30]), while the year with the lowest growth was 2020 in the post treatment period (4.37 [4.05 – 4.71]). The variance in growth was higher among individual shoots than among plots. The total random variation accounted for 15.1 % of the total residual variation, with 8.4% being associated with difference in shoot length within a plot, and 6.7% accounts for the between plot variation. The difference between minimum and maximum increment length within the six years of measurement are large (min= 0.4 mm, max=97.0 mm, n=3748). Side shoot initiation have increased by 177 % compared to pre-treatment period (Fig. A2, Appendix), while the number of dead tips has stayed consistent in all six years (Table A4, Appendix).

The shoot growth Increment of controls decreased by 11% after being transplanted to the garden in 2018. Transplant and treatment happened in sequence, with the post-treatment period defined between 2019 and 2021. If growth was not impacted by treatment, we would expect the rest of the plots to have a similar decline following transplantation. Instead, thaw-freeze growth increments increased their length by 19.8% compared to pre-treatment, and 30.5% compared to the expected estimate following transplantation (Fig. 4B). Similarly, icing growth increments has increased by 1.9% compared to pre-treatment, but the effect of icing is closer to 12.6%.



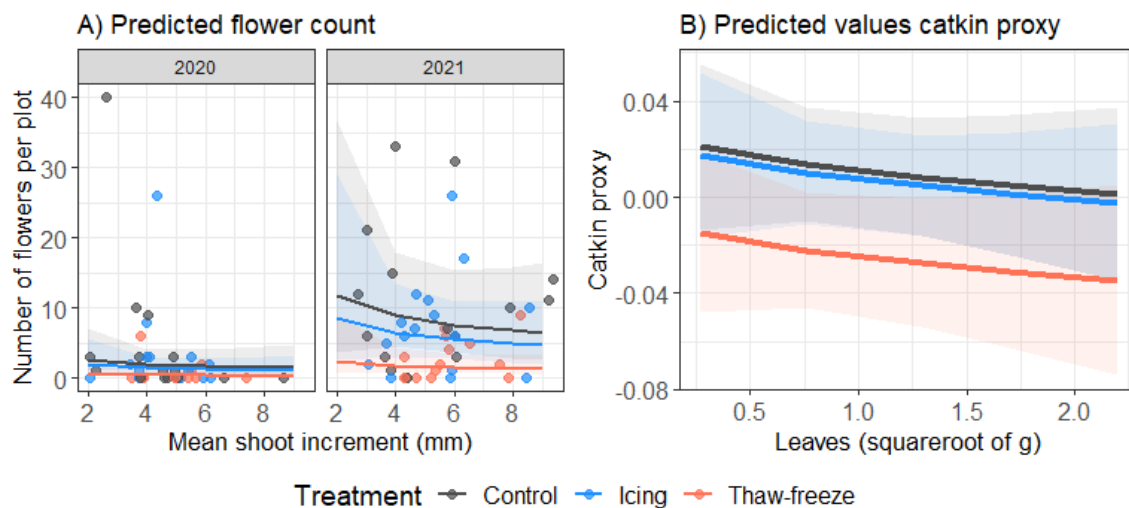
**Figure 4** A) Timeline of predicted mean shoot increment growth of *S. polaris* in the garden for each treatment with the line indicating transplant. Note that Thaw-freeze did not receive treatment in 2019 B) Estimated annual shoot growth increment for *S. polaris* three years before the treatment period and the three years during the treatment period. The black arrow illustrates the effect of transplantation on control plots, with the transparent points of icing and thaw-freeze in post-treatment illustrating how the estimated means would have been with only transplant affecting the increment. The orange arrow illuminates the treatment effect explained by the interaction coefficient between treatment and the period. C) Estimated mean flower count for *S. polaris* in the garden.

### 3.1.2 Yearly reproductive traits of *S. polaris*

Flower count varied greatly between years (fig. 4C). Though flower count had a slight decrease from 2019 to 2020 the estimated mean increased fourfold from 2020 to 2021. The highest flower count was observed in a control plot in 2019 (max=59).

For every 30% increase in shoot growth increment, the flower count decrease by 10% (Fig. 5A) in *S. polaris*. The effect of treatment and year are larger but pulling in different directions. Thaw-freeze had five times less flowers compared to controls in 2021 with a ratio of 0.2 [0.3-- 1.8], and the mean of controls alone increase with nearly the same amount from 2020 (1.9 [0.9- 4.0]) to 2021 (8.1 [4.2-15.7]). Icing has less effect on flower count than thaw-freeze, with much variation around the mean flower count especially in 2021 (5.9 [3.0-11.4]). Mean number of flowers in icing has not changed much from 2019 to 2021 with a ratio of 0.9 [0.8 - 1.0], nor is it different from controls in 2019 (ratio= 1.03 [0.9 - 1.2]) (Table B7, Appendix B)

The additive model presented here with growth increment, treatment and year as predictors ranked higher in the model selection than a model with the same predictors but with interaction between increment and treatment ( $\Delta AIC_C = 3.48$ , Table 1). This result show there is no evidence for changes in trade-off due to treatment, though both icing and thaw-freeze has a negative effect on flower number to different degrees as described above.



**Figure 5** A) Predicted flower count of *S. polaris* per plot by shoot increment in 2020 and 2021. Points are observations. B) Estimated values of the catkin biomass proxy by the weight of leaves. The proxy is residuals from a linear model with predicting the weight of catkins per plot with number of catkins per plot as predictor.

### 3.1.3 Leaf and catkin biomass in 2021

As with increment, the biomass of leaves varies greatly between plots in the garden (0.8 g [0.7 – 1.0], max=2.24 g, min= 0.02 g). The icing and thaw-freeze treatment did not affect the amount of leaf biomass produced in each plot (Table B3, Appendix B). Large variation of catkin weight was observed as well (20 mg [10 – 30], max= 160 mg, min= 2 mg), including much variation in the number of seed capsules per catkin (3.8 [3.3 – 4.4], max= 17, min=1). Catkin number per plot highly correlates with the weight of catkin per plot ( $r= 0.87$  [0.75-- 0.94],  $df= 30$ ), and so does the total number of seed capsule per plot ( $r= 0.87$  [0.75-- 0.94],  $df= 30$ ). Therefore, the following model will be based on a catkin biomass proxy where I use the residual of the relation between the count of catkins and catkin weight on plot level (See Statistical Methods )

The weight of leaves decrease with increasing catkin proxy values (i.e., reproductive effort of *S. polaris*, ig. 6B), and the slope was similar across treatments. Hence, the additive model was ranked higher in model selection in comparison to a model where leaf weight and treatment interacted ( $\Delta AIC_c= 2.34$ , Table 1). As such, there is no evidence for treatment mediated trade-off influencing the negative trend between the catkin proxy and the weight of leaves. For a given catkin proxy value, thaw-freeze plots had lower leaves weights (lower intercept (-0.04 [-0.07 – -0.00])), compared to controls (0.03 [-0.03 – 0.09])). The intercept from icing is not different to controls. With thaw-freeze having negative catkin proxy values, this indicate lighter catkins in relation to the number of catkins.

Response	Variables	<i>df</i>	AIC <sub>C</sub>	ΔAIC <sub>C</sub>
<i>S. polaris</i> flower count	<b>Log(increment) + treatment + year</b>	<b>7</b>	<b>443.70</b>	<b>0.00</b>
	Log(increment) * treatment + year	9	447.18	3.48
<i>S. polaris</i> catkin proxy	<b>Sqrt(leaf weight) + treatment</b>	<b>5</b>	<b>-135.57</b>	<b>0.00</b>
	Sqrt(leaf weight) * treatment	7	-129.57	6.00
<i>C. tetragona</i> flower count in 2020	<b>Proportion of alive side-shoots + treatment</b>	<b>4</b>	<b>377.58</b>	<b>0.00</b>
	Proportion of alive side-shoots * treatment	5	379.92	2.34

**Table 1:** Model selection to test for treatment mediated trade-off. None of the models with interaction (indicated by \*) between vegetative predictor and treatment had significant predictors, meaning there is no evidence of change in trade off with treatment. Increment is the logged shoot growth increment of *S. polaris*, and treatment for *S. polaris* contain control, icing, and thaw-freeze. Treatment in *C. tetragona* is only control and icing. Proportion of alive side shoots is in contrast to dead side-shoots. All of analyses are performed on data from the common garden.

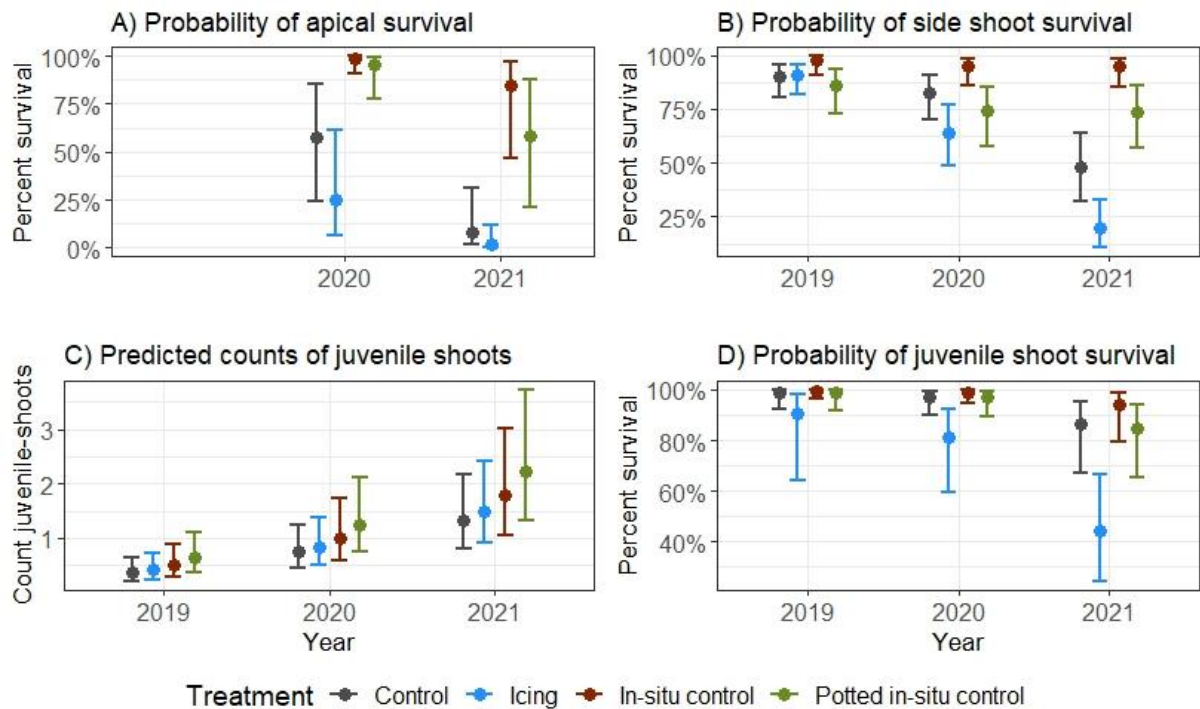
## 3.2 *Cassiope Tetragona*

### 3.2.1 Yearly vegetative traits in *C. tetragona*

The number of living apical shoots in the garden declined in both 2020 and 2021. Shoots experiencing icing had a 24.7% chance to survive in 2020, and a cumulative probability of 2.1% to survive in 2021 (Fig. 6A). For control plots, the probability to survive is 57.8% and 8.2% respectively. Note that all apical shoots were alive in 2019. All plots in the common garden had a drastic decrease in shoot survival compared to the in-situ controls, but this is most pronounced following the icing treatment.

The same is true for side-shoot survival. The icing treatment caused a decrease in survival probability from 64.0% to 19.6% between 2020 and 2021 (Fig. 6B). This contrasts the control plots which decreased from 82.7% to 47.9%. Icing has a steeper decrease in survival compared to the controls as it interacts with year in both 2020 and 2021. Despite this decrease in survival probability, the count of juvenile side shoots has increased in both icing plots and controls by more than threefold (Fig. 6C). All the control groups have higher counts of alive juvenile side-shoots compared to icing plots. A reason may be that the survival probability of juvenile side-shoots following icing treatment is lowered by 50% (Fig. 6D). We do see a trend of higher total shoot count of both alive and dead juvenile side-shoots in icing, with there being 61.2% higher counts of juvenile side-shoots in icing plots compared to controls.

Both growing in a pot and growing in the common garden has overall affected all the measured traits in *C. tetragona*, as both shoot survival, count and flower count is higher in the undisturbed in-situ control (Fig. 6 and 7). In 2021, the difference in probability of apical shoot survival between in-situ control and the potted in-situ control is 36.4%. For side-shoot survival that difference is 24.8%. Being transplanted and growing in the garden also affect the overall shoot survival. If we compare the control in the garden to the potted control in-situ, the difference in apical survival is 150.6% in 2021. For side-shoot survival in 2021, that difference in survival probability is 42.7%.

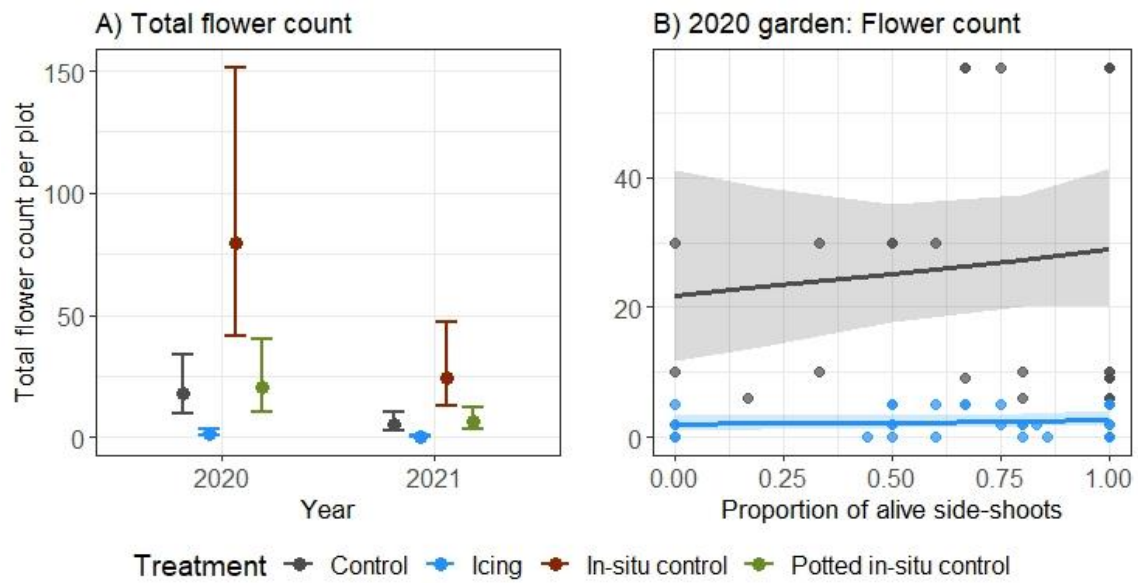


**Figure 6** A) Predicted cumulative probability of apical survival of *C. tetragona* on in the garden and in-situ. 2019 excluded as shoots were selected to be alive. B) predicted cumulative probability of *C. tetragona* side shoot survival, note that both 2020 and 2021 is compared to 2019. C) predicted count of juvenile side-shoots of *C. tetragona* per plot, showing shoot recruitment and D) predicted cumulative probability of *C. tetragona* mini shoot survival per year

### 3.2.2 Yearly reproductive traits in *C. tetragona*

We see large yearly variation in flower count just between 2020 and 2021, also in the in-situ groups (Fig. 7A). Only 2/12 plots in the garden had flowers in 2021 and both were controls. Therefore, the following model will only contain counts from 2020. In that season, icing plots also had a low flower count per plot (2 [1.6-3.4]) compared to controls (27 [19.7-36.0]), which has 13 times more flowers per plot. Though we see a strong “treatment effect”, there is less of a relationship between the proportion of alive side shoots and flower count. It has a slight positive slope ( $\beta=0.28$  (log) [-0.50 – 1.03]), compared to the negative effect of icing ( $\beta=-2.42$  (log) [-2.91 – -1.94]).

Interaction between proportion of alive side-shoots and treatment was tested in a model selection together with an additive counterpart (Table 1). It had no significant interactions and with higher AICc than the additive model (AICc=  $\Delta 2.34$ ). Therefore, we cannot prove an icing mediated trade-off between the proportion of alive shoots and flower count in *Cassiope*.



**Figure 7** A) Predicted total flower count of Cassiope in both the common garden and in-situ for 2020 and 2021, B) predicted flower count in the common garden by the proportion of alive side shoots in 2020. The dots are observed number of flowers per plot along the proportion of alive side shoots.



## 4 Discussion

In this study I aimed to investigate whether and how basal ice and thaw-freeze simulation affected vegetative and reproductive traits, and the trade-offs between them, in two high-Arctic shrubs with contrasting growth forms (i.e., deciduous *versus* evergreen). I found no evidence for treatment mediating trade-offs between shoot increment growth and flower number or between leaf weight and the reproductive investment (i.e., catkin proxy) in *S. polaris* (Fig. 7, Table 1). Nor did I find that icing affected trade-off between proportion of alive shoots and flower number in *C. tetragona* (Fig. 10B). Still, treatments influenced the specific variables. For *S. polaris*, icing increased shoot growth increment to some degree (Fig. 4C), slightly decreased number of flowers but did not cause lighter catkins. Thaw freeze had a larger impact on these variables, in addition to causing lighter catkins. In *C. tetragona*, icing had a large impact by reducing shoot survival (Fig. 9) and flower number. Despite the reduced probability of survival in both apical shoots, side-shoots and juvenile side-shoots of *C. tetragona*, a higher number of juvenile side-shoots following the icing treatment indicated compensatory growth.

### Treatment does not affect trade-off in neither species

Contrary to expectations, we did not see any convincing evidence of treatment mediated trade-offs between vegetative and reproductive traits in either species. In *S. polaris*, thaw-freeze increased shoot growth increment more than icing, and we can assume more energy is allocated to vegetative growth in these shoots. Coupled with the fact that there is less flowers in plots treated with thaw-freeze compared to icing and controls, it is surprising that we do not see any evidence of a treatment mediating the trade-off in these plots. *S. polaris* also reproduce asexually through stolons and runners (see rightmost side-shoot in Fig. A1, Appendix A), this may particularly happen being in stressed environment. This potential change in reproductive strategy may mask the effect of treatment on resource allocation.

The mentioned elongation of increment is analysed on shoot level but has been upscaled to plot means to match the plot level of flower number. That might be a reason why I did not detect treatment mediated trade-offs between these two variables, and I expect the influence of treatment may happen on smaller scales (i.e. number of flowers per shoot). This lack of treatment effect is in line with the discussion of Le Moullec et al. (2019) regarding how the potential changes in trade-off in energy allocation for *S. polaris* may be limited as they found few direct effects of icing treatment on the relative abundance and flower count on this species in particular. However, they did find larger effects on other traits (i.e. flower phenology and specific leaf area (SLA)), suggesting that icing might influence the trade-off between other traits than measured in this study.

In *C. tetragona*, icing decreased both shoot survival and flower count in 2020, similarly to Milner et al. (2016). It may be that icing decreased the traits to a similar degree, not affecting the slope of their relationship, i.e. the trade-off. Alternatively, the low number of flowers in iced plot regardless of shoot survival may indicate that the large effect of icing on the flowering of *C. tetragona* leaves little room for the vegetative predictor to influence. In addition, the large variation of both variables in control plots may have prevented me to find a clear pattern. Previously, flower production has been negatively correlated to vegetative growth the same year (Johnstone and Henry, 1997). As such, survival of shoots may be less correlated to vegetative resource allocation than shoot growth. Therefore, icing may have a greater impact on the trade-off between flower count and shoot increment growth, e.g., measured between wintermark septa (Myers-Smith et al., 2015). As I have only measured a subset of internal allocation options, my results does not exclude trade-off between other reproductive (i.e. seed production, dry weight of flowers) and vegetative (i.e. leaf production) traits.

The overall absence of *C. tetragona* flowers in 2021 may be connected to the unusually high flowering across species in 2020 that was observed across species in Adventdalen (Le Moullec et al. (2021)). Flower bud formation occur the previous season (Semenchuk et al., 2013), and flowering may have been prioritized the previous year (ref). Hence, investment in flower production and formation of new flower buds may not be prioritized simultaneously in *C. tetragona*. This made me unable to demonstrate the likely lag effect of icing on trade-off, where I would expect to see higher proportion of alive shoots in relation to the low flowering of *C. tetragona*.

#### Larger effects of basal ice in *C. tetragona* than *S. polaris*

The low survival of apical shoots and side-shoots in *C. tetragona* following basal ice has also been observed in-situ following ROS and basal ice formation by Bjerke et al. (2017) and experimentally by Milner et al. (2016) in a one-year experiment. The latter found that previously healthy shoots were damaged, but not necessarily dead following one season of basal ice. Here I show the effect of increased mortality following a second round of basal ice simulation, as mortality was higher in 2021 compared to 2020. This increase in mortality levels over time has also been observed in the sub-Arctic (Preece et al., 2012). In contrast, icing does not seem to affect shoot survival for *S. polaris* (Le Moullec et al., 2019, Bjerke et al., 2018). However, it is important to note that the number of dead shoots may be underestimated due to the pre-selection process of *S. polaris* shoots for analysis. *C. tetragona* compensate shoot damage by investing in new shoots (Milner et al., 2018). Here the second year of treatment severely affected the survival of juvenile side-shoots, illustrating the impacts on the recovery of *C. tetragona* following multiple ROS events. The

large increase in side-shoot numbers of *S. polaris* across plots may be a response to the new conditions experienced in the garden (i.e., drier, and warmer soils, pers. Obs.). Although it was apparently not a response to treatment nor shoot death, it showcase the resistance of juvenile side-shoots to basal ice in *S. polaris*.

Overwintering flower buds are vulnerable to environmental conditions (Semenchuk et al., 2013). In addition to the direct effects of icing on flowers, icing may indirectly affect flower abundance if the number of alive shoots reduce. *C. tetragona* thus had a steeper decrease in flower numbers following icing treatment than *S. polaris*. The low number of flowers in 2020 and the complete lack of flowers in 2021 in iced plots demonstrate the severe effect basal ice can have on the reproduction of *C. tetragona*. In contrast, the flowering of *S. polaris* shows high resilience after three years of consecutive icing.

Basal ice can cause delay in spring onset and affect the soil temperature regime by stagnating the temperature to  $\sim 0^{\circ}$  Celsius during snowmelt, and then delaying further soil temperature increase (Le Moullec et al., 2019). Although this phenomenon remain to be investigated in this common garden where plots are surrounded by exogenous soils, this, along with the potential physiological effects such as ice driven anoxia and desiccation (Andews, 1996) seem to be within what *S. polaris* can handle. *C. tetragona* on the other hand has a much greater extent of its biomass covered in ice. Being an evergreen shrub, they do not regrow damaged leaves and therefore appear more vulnerable. Furthermore, the different responses to the icing treatment in *S. polaris* and *C. tetragona* may be due to their different life history traits and survival strategies during winter. As *S. polaris* has most of their biomass below ground and in the moss layer, they are largely protected against coming into direct contact with the ice.

#### Thaw-freeze has higher impact than basal ice on *S. polaris*

Thaw-freeze increased the length of growth increments in *S. polaris* more than icing. In this case, a possible mechanism could be related to stress, as thaw-freeze impacts the shoots by de-acclimatising them. This initiate metabolic processes associated to spring (Rapacz, 2002) and may cause them to be more vulnerable when normal winter temperatures return. This could stress the meristems responsible for growth (Inouye, 2001). In contrast, the basal ice simulation affects the plants when they are still in dormancy, and that might be why they can handle the ice encasement to a higher extent. Increase in shoot length has also been observed in some sub-Arctic species such as the deciduous shrub *Vaccinium myrtillus* and evergreen *Empetrum hermaphroditum*, following a thaw-freeze simulation where they thawed by infrared heating lamps (Bokhorst et al., 2011).

In the same experiment, (Bokhorst et al., 2009) found increased mortality of shoots, contrasting the low shoot death in *S. polaris* following thaw-freeze. In addition, Bjerke et al. (2018) found a much higher proportion of wilted shoots after a late spring frost simulation. Their simulation could be comparable to our thaw-freeze treatment as both expose the plants to a period of thawing followed by freezing temperatures. However, they performed this in April on juvenile *S. polaris* and the plants may have already been out of dormancy when they returned to freezing temperatures.

Leaf growth is an important use of resources. Icing and thaw-freeze did not affect the amount of leaf biomass produced in 2021. This brings forth the question of why leaf mass is not affected by thaw-freeze, but increment is. There are many vegetative traits that *S. polaris* can allocate energy to, and here they seem to prioritize stem elongation over leaf production in response to the stress imposed by thaw-freezing events. Røssum (2022) found a slight increase in the ratio between below- and above ground biomass in *S. polaris* following basal ice and suggested this might be due to a slight increase in below-ground biomass. Growth below- and above ground can have different sensitivity to climate (Ropars et al., 2017), and intra-plant energy allocation to vegetative growth in *S. polaris* seem to be regulated in part by temperature (Buchwal et al., 2013). This include temperature of the previous season, as stored energy from the previous year initiate and influence increment elongation in closely related *Salix* species such as *Salix herbacea* (Wijk, 1986). This prompts the question of whether icing can modulate trade-off between two vegetative traits (i.e. root growth and stem increment), masking the effect on a single trait. In addition, perhaps a reason to why I do not detect effect on leaf biomass may be that the influences are on other leaf characteristics such as those reflected by specific leaf area (SLA), which is a proxy of leaf growth rate. Indeed, Le Moullec et al. (2021) found that leaves of *S. polaris* are smaller and lighter following icing treatment, although maintaining similar relative abundances to controls. The difference in scale (i.e. total leaf biomass *versus* individual shoots) may mask the effects of treatment.

The thaw-freeze treatment seemed to lower reproductive effort (i.e. flower count and catkin proxy) further than icing in *S. polaris*. The drivers of this difference in response are likely similar with the ones related to shoot increment, as discussed above. Bokhorst et al. (2011), in their sub-Arctic thaw-freeze experiment, observed a significant lowering of reproductive effort both in terms of flowering for *V. myrtillus*, but not for *E. hermaphroditum*. Their species dependent results align with mine, but contrasts in that they see an effect on the deciduous species, rather than the evergreen species as I do.

### Wider implications of ROS and warm spells

Currently, basal icing is a major environmental event occasionally affecting the plant community on Svalbard (Bjerke, Le Moullec, etc.). Based on my results it may seem that *S. polaris* is better equipped for a future of more extreme climatic events, as it is a hardy species with less biomass exposed above-ground, than e.g. *C. tetragona*. *C. tetragona* seem more vulnerable to basal ice, but the response to thaw-freeze events remain to be studied. *C. tetragona* grow where they are protected by deep snowpack. Rain and melted snow during ROS events may typically not reach the bottom of deep snowpacks (Peeters et al. 2019), thereby not impacting *C. tetragona*. However, if ROS intensity and warm spell frequency increase as projected, deep snowpack may not be enough to protect them (ref Bjerke paper?).

Projected summer warming is also occurring alongside winter warming (Hanssen-Bauer et al., 2019). This may increase growth and has thus been linked to Arctic greening (van der Wal and Stien, 2014, Hudson et al., 2011). *S. polaris* showed increased increment length response to icing and especially thaw-freezing, but summer warming and its effects on productivity might modify this process. The Le Moullec et al. (2021) study from a similar mesic community demonstrated an increased productivity of *S. polaris* following simulated icing, largely enhanced when combined with experimental summer warming. Summer warming and winter warming impact vegetation on two different temporal scales (Niittynen et al., 2020), which may impact the spatial pattern of co-fluctuations in growth of *S. polaris* as summer temperatures synchronize growth while winter warming events may disrupt this spatial synchrony (Le Moullec et al., 2020). *C. tetragona* on the other hand has apparently suffered large die-backs in some years due to icing events (Bjerke et al., 2017), including in the study site from which we selected our plots. While they may compensate by growing new side shoots (Milner et al., 2016) it can be hard to recover, as this study underlines. Thus, because episodic extreme winter warming and rain-on-snow events are becoming the rule rather than the exception, this may contribute to shape community composition in the future, and impact both vegetation and higher trophic levels.

### Limitations of the experimental approach and data

The use of common garden as experimental approach brings many benefits such as the ability to keep higher control of variables that are outside of our interest. The plots can experience similar abiotic factors such as weather, and measurements can be done in quick succession to lessen the variation of time in our data. However, when we take plots of tundra out of its natural habitats and into a pot, this might have some unintended consequences. This is especially highlighted in *C. tetragona*, as shoots in-situ have much

higher survival and number of flowers than in garden controls (analyses not presented), probably since main roots have been cut during the transplanting process. As for *S. polaris*, shoot growth increments of controls plots also decreased after transplant to the garden, this may also reflect shoot damage to some extent. The pot limits lateral water transfer, so the soil moisture levels is lower than in-situ (analyses not presented). However, to mitigate drought, we watered the plots regularly. Some of the plots come from waterlogged habitats, and therefore nevertheless experience drier conditions in the garden which might contribute to the decreased shoot increment growth in *S. polaris*.

Missing (or missed) years of increment growth are not unlikely, as this is observed in radial growth rings (Buchwal et al., 2013). Here, missing growth increments seem to stem from damage or death to the tips, rather than lack of growth within a year (pers. obs). When this occurs, scars from the broken stem are visible and the new growth initiated below is labelled as side-shoots. Unless I could verify the age of the old shoot, it was not measured. The main way to ensure that the growth is linked to the correct year was by comparing number of increments with side shoots growing below. This was done during the measurement process when such scars of broken stems were detected, and I believe the precision of this method was adequate and did not affect the results.

## 5 Conclusion

This common garden approach has enabled me to simulate and compare outcomes of ROS and episodic warm spells during winter in two Arctic shrubs. Through this study I found no evidence of icing and thaw-freeze changing the trade-offs between vegetative and reproductive traits. Though *S. polaris* appear less damaged and rather increase growth, *C. tetragona* showed high shoot mortality and seemed to struggle to compensate through shoot initiation. Both species decreased their number of flowers under icing, but this decrease was more dramatic for *C. tetragona*. However, thaw-freeze proved as harsher treatment for *S. polaris* than icing, and future studies should look into the effects of such events on *C. tetragona* as well. This study nevertheless demonstrates the differential response species has to extreme winter events and adds to the complexity of the ongoing greening and browning in the Arctic. With the projected increase in ROS and warm spells during winter, community wide effects might be expected, possibly as reduced abundance of *C. tetragona* in particular.

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## 8 Appendices

### Appendix A: supplementary tables and figures

	Icing		Thaw – freeze	Control	
2019	22 <i>Salix</i>			37 <i>Salix</i> (+ 32 <i>in situ</i> )	
2020/-21	22 <i>Salix</i>	6 <i>Cassiope</i>	15 <i>Salix</i>	23 <i>Salix</i> (+ 32 <i>in situ</i> )	6 <i>Cassiope</i> (+ 10 <i>in situ</i> )

**Table A1:** Organization of treatment and species in the common garden between 2019 and 2021. Note that the number of controls has decreased from 2019 to 2020. Thaw-freeze were performed in 2020 and 2021 on 15 plots that were controls in 2019. Of the plots *in-situ*, half are in a pot and half are undisturbed tundra.

Year	total side shoots monitored	Alive apical shoot	Side shoot alive	Side shoot dead	Juvenile shoot alive	Juvenile shoot dead	Flower count	Absence of flowers
2021	146/119/161	4/19/15	43/65/57	52/4/22	44/48/73	7/2/9	17/126/82	0/0/0/
2020	128/97/120	17/24/21	80/67/60	23/4/23	24/24/33	1/2/4	169/435/114	4/0/0/
2019	121/98/97	30/25/25	93/77/70	14/2/13	13/19/13	1/0/1	NA	NA

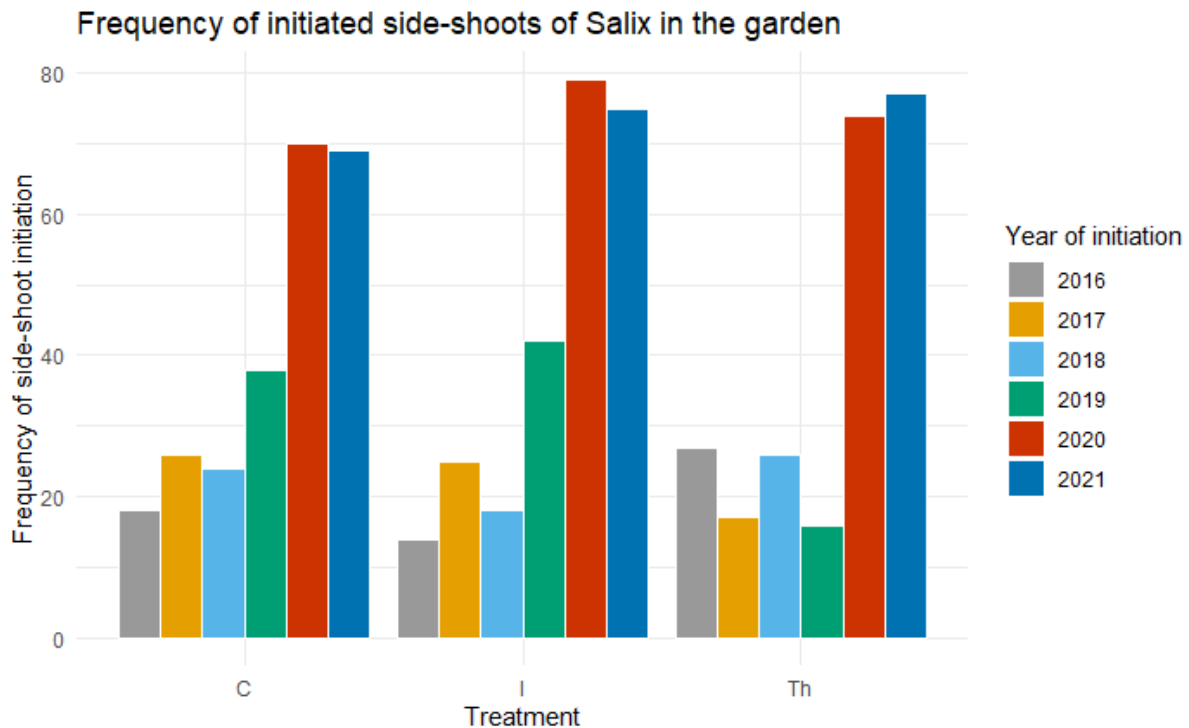
**Table A2:** summary table of all the controls of *C. tetragona*, both in the garden and *in situ*. The format of the values is garden controls/*in-situ* C/*in-situ* C-P. *Total side shoot monitored* represent the total number of surveyed side shoots. *Alive apical shoot* is the total number of alive apical shoots of the shoots monitored. Of the *side shoots: alive/dead* and *juvenile shoots: alive/dead* the total number of alive to side shoots respectively. *Flower count* is the total number of flowers in the garden, and *absence of flowers* are plots without any flowers.

<i>Salix polaris</i>			<i>Cassiope tetragona</i>					
Year	Plots / shoots / increments	Initiated shoots/dead tip *	<i>S. polaris</i> present / absence of flowers / Flower count	Shoots marked / total side shoot monitored	Alive apical shoot	Side shoots: alive / dead	Juvenile shoots: alive / dead	Flower count / absence of flowers
<b>2021</b>	45 / 237 / 922	221/182	73 / 9 /407	57/360	4	65/141	85/69	17/10
<b>2020</b>	46 / 250 / 797	222/215	71/23/144	59/291	28	157/67	62/5	185/2
<b>2019</b>	46 / 246 / 608	96/219	72/18/251	60/259	60	204/26	28/1	NA
<b>2018</b>	46 / 247 / 528	67/218	74/NA/NA					
<b>2017</b>	46 / 234 / 461	59/199						
<b>2016</b>	46 / 231 / 379	21/182						

**Table A4:** Summary table of *Salix polaris* and *Cassiope tetragona* between 2016 and 2021 in the common garden. The period of 2016-2018 is before the experiment and transplantation. Of *S. polaris*, *plots* refer to the number of plots shoot increment samples have been sampled from, *shoots* is the total number of shoots sampled, *increment* is the total number of increments measured. *Initiated shoots* are how many of the measured shoots initiated that specific year, and *dead tip* is how the many shoots are recorded as dead per year. *S. polaris present* is how many plots in the garden have *S. polaris*, *absence of flowers* are how many plots has an absence of flowers, *flower count* shows the total number of *S. polaris* flowers that has been recorded. Of *C. tetragona*, *shoots marked* are the total number of selected shoots, the decrease show missing shoots. *Total side shoot monitored* represent the total number of surveyed side shoots. *Alive apical shoot* is the total number of alive apical shoots of the shoots monitored. Of the *side shoots: alive/dead* and *juvenile shoots: alive/dead* the total number of alive to side shoots respectively. *Flower count* is the total number of flowers in the garden, and *absence of flowers* are plots without any flowers.



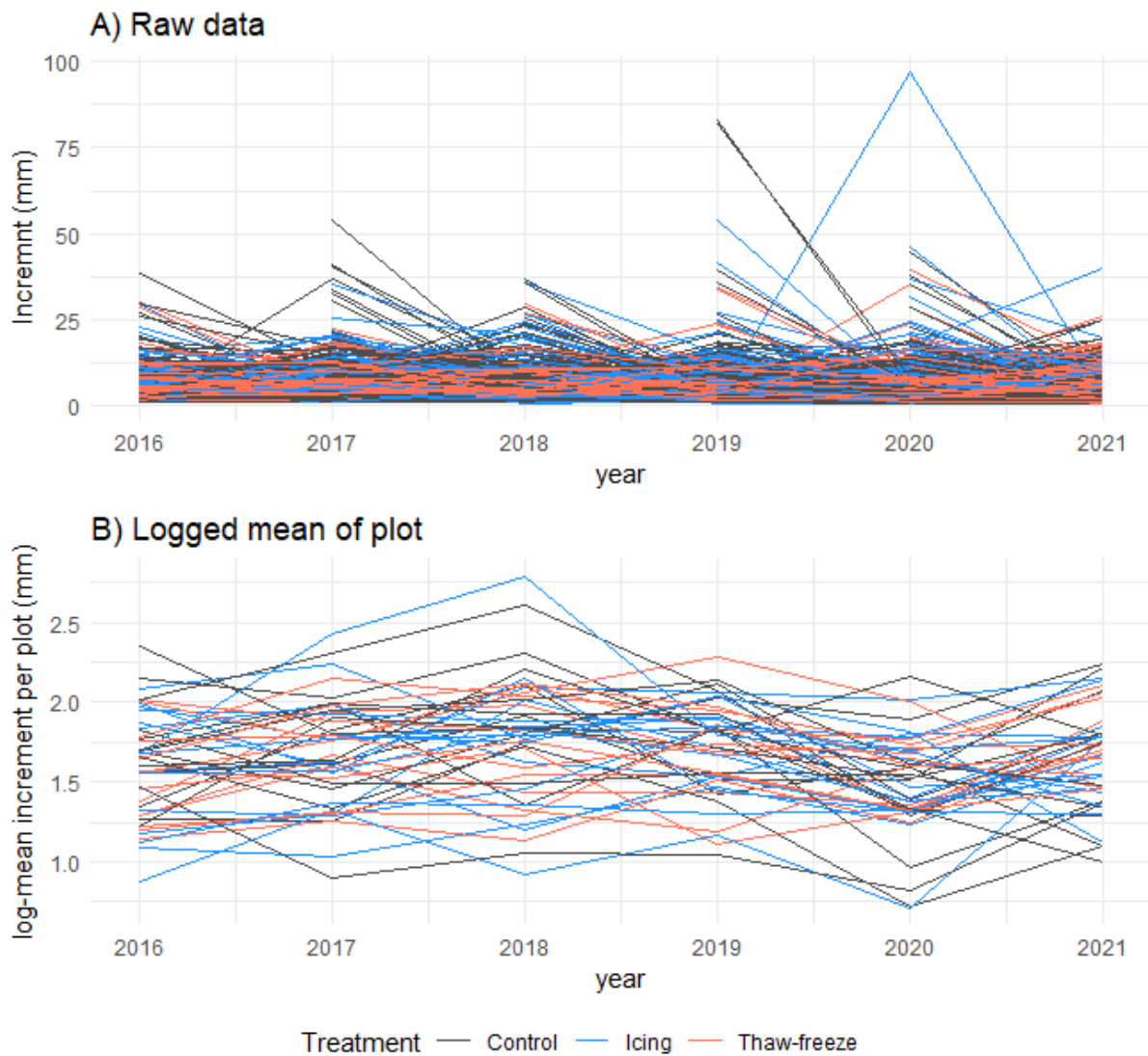
**Figure A1** A picture of an individual shoot with attached side shoots illustrating the different increment lengths and state of side shoots. From the left: main shoot, side shoot with two increments, two dead side shoots and a runner/stolon that has been below the moss layer and may have barely poked aboveground due to the green tip. B) Picture of a *S. polaris* side shoot with two attached catkins. The grey, hairy outgrowths are seed capsules. In the corner of both figures are millimeter paper for scale. C) Pipe (19.5 cm diameter) subdivided into four by a string. This was used during the flower count of *S. polaris*.



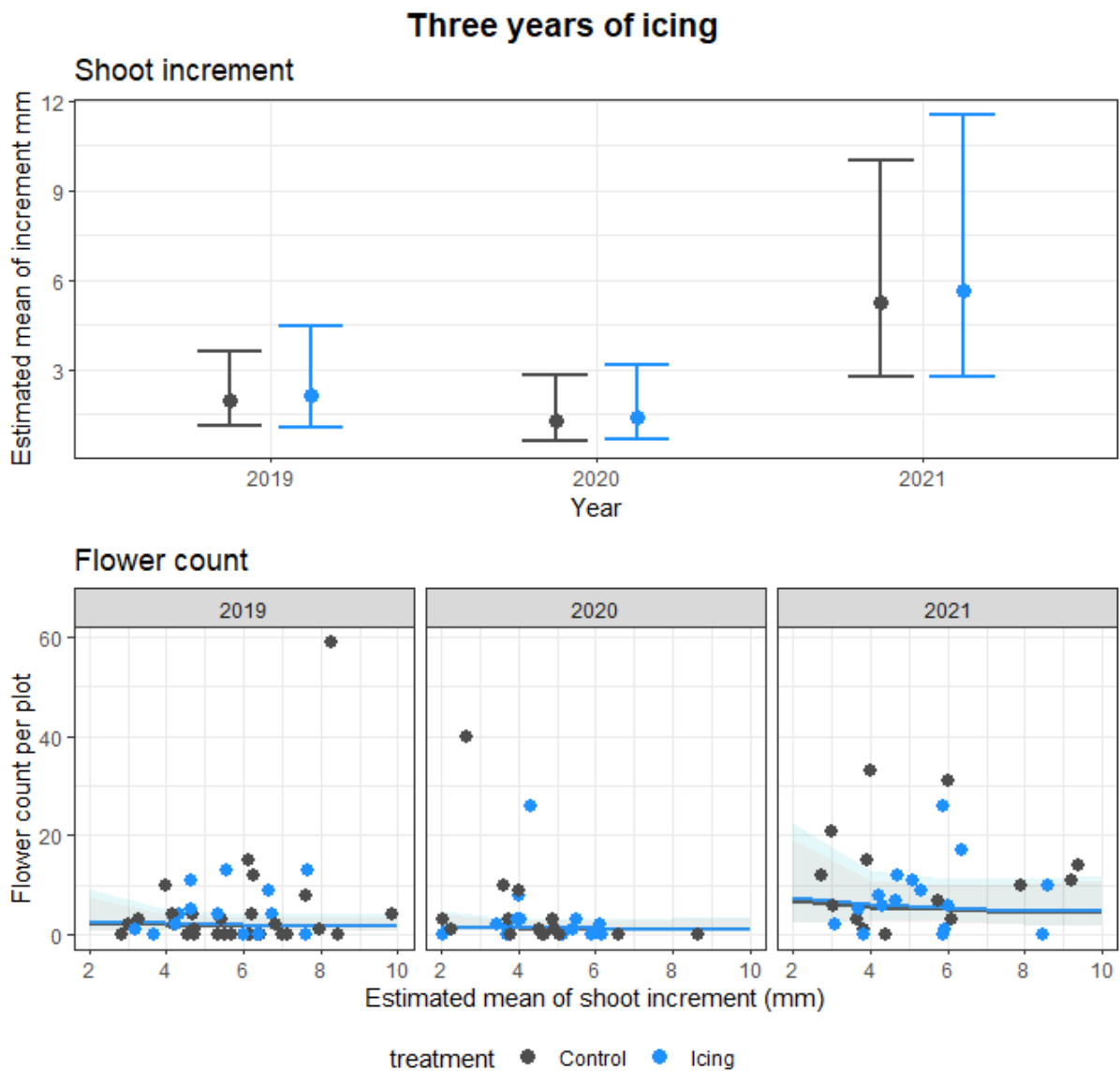
**Figure A2** A figure displaying the frequency of the frequency of initiated side shoots of *S. polaris* in the garden between 2016 and 2021. The period between 2016 and 2018 is before the experiment and transplantation. Note the large, even increase in new side shoots across treatments in 2020 and 2021. C = Control, I = Icing, Th = Thaw-freeze.



### Time series shoot of increment



**Figure A5:** Timeseries of shoot increment between 2016 and 2021, note that the period between 2016 and 2018 is before the experiment and transplantation. A) plotted of raw data of yearly length (mm) of each side-shoot. New lines indicate the start year of measurement for that individual side-shoot, either because it initiated that year or because the increments below could not be read. B) The timeline of plot level increment (log of mm), after the mean per plot length has been estimated through an LMM, with year (2016-2021) × plot ID predicting increment on log-scale. Random intercept was shoot ID nested in plot ID.



**Figure A6:** Three years of icing on *S. polaris* A) Estimated mean of shoot increment by LMM with year (2019-2021) + treatment (I, C) as predictors of logged shoot increment (mm). Random structure is shoot ID nested within plot ID. B) Estimated slope of how flower count changes with increment. Raw data in the background. Estimated in GLMM with treatment (C and I) and year (2019 - 2021) as predictors. As there was sign of over dispersion I used a negative binomial distribution with log link. C = control, I= Icing.

## Appendix B: Model outputs

**Table B1:** Timeline with the estimated mean of *S. polaris* shoot increment (log of mm) per year per treatment between 2016 and 2021. Predicted from an LMM that include year × treatment, with random intercept set at shoot ID nested within plot ID. Included are standard error (SE), degree of freedom (*df*), lower confidence limit (lower.CL) and upper confidence limit (upper.CL), the two former are calculated from 95% confidence interval. C = Control, I = Icing, Th = Thaw-freeze.

Year	Treatment	Estimated mean (log)	SE	<i>df</i>	lower.CL	upper.CL
2016	C	1.67	0.08	180	1.41	1.94
	I	1.63	0.08	202	1.37	1.88
	Th	1.54	0.08	160	1.27	1.81
2017	C	1.74	0.08	142	1.49	1.99
	I	1.68	0.07	159	1.43	1.92
	Th	1.67	0.08	135	1.41	1.92
2018	C	1.88	0.07	122	1.64	2.12
	I	1.70	0.07	141	1.47	1.94
	Th	1.69	0.08	116	1.44	1.94
2019	C	1.76	0.07	105	1.52	1.99
	I	1.72	0.07	119	1.49	1.94
	Th	1.65	0.07	109	1.40	1.89
2020	C	1.42	0.07	86	1.19	1.64
	I	1.47	0.06	92	1.25	1.68
	Th	1.55	0.07	87	1.31	1.78
2021	C	1.57	0.07	77	1.36	1.79
	I	1.63	0.06	86	1.42	1.84
	Th	1.78	0.07	79	1.55	2.01

**Table B2:** Model output with estimates on the original log-scale of the shoot increment of *S. polaris* before and after transplant and treatment. From an LMM with period (pre- /post treatment) × treatment as predictors, and random intercept is set at year (2016-2021) and shoot ID nested within plot ID. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing, Th = Thaw-freeze.

<i>Predictors</i>	<b>log(increment)</b>		
	<i>Estimates</i>	<i>95% CI</i>	<i>p</i>
(Intercept) [C]	1.73	1.57 – 1.89	<b>&lt;0.001</b>
treatment [I]	-0.10	-0.27 – 0.07	0.236
treatment [Th]	-0.14	-0.32 – 0.03	0.105
period [post-treatment]	-0.11	-0.25 – 0.02	0.096
treatment [I] * period [post-treatment]	0.13	0.02 – 0.24	<b>0.022</b>
treatment [Th] * period [post-treatment]	0.29	0.17 – 0.41	<b>&lt;0.001</b>
<b>Random Effects</b>			
$\sigma^2$	0.48		
T00 whole_shoot_id:plot	0.04		
T00 plot	0.03		
T00 year	0.01		
ICC	0.16		
N year	6		
N whole_shoot_id	254		
N plot	46		
Observations	3748		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.006 / 0.161		

**Table B3:** Model output with estimates on the original log-scale of the flower number of *S. polaris* in 2020 and 2021. From an LMM with year  $\times$  treatment as predictors, and random intercept is set at plot ID. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing, Th = Thaw-freeze.

<i>Predictors</i>	<b>Flower number (log)</b>		
	<i>Log-Mean</i>	<i>95% CI</i>	<i>p</i>
(Intercept)[C]	1.26	-0.29 – 2.81	0.112
increment[log]	-0.40	-1.43 – 0.64	0.452
treatment[I]	-0.32	-1.21 – 0.57	0.478
treatment[Th]	-1.61	-2.59 – -0.62	<b>0.001</b>
year[2021]	1.48	0.93 – 2.02	<b>&lt;0.001</b>
<b>Random Effects</b>			
$\sigma^2$	0.70		
T00 <sub>plot</sub>	1.02		
ICC	0.59		
N <sub>plot</sub>	45		
Observations	89		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.372 / 0.743		

**Table B3:** Model estimates from an LM predicting the weight of *S. polaris* leaves (square root, g) with treatment as predictor. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing, Th = Thaw-freeze.

<i>Predictors</i>	<i>Estimates</i>	<b>Leaves (sqrt)</b>	
		<i>95% CI</i>	<i>p</i>
(Intercept)	0.93	0.79 – 1.06	<b>&lt;0.001</b>
treatment [I]	0.00	-0.18 – 0.19	0.959
treatment [Th]	-0.04	-0.25 – 0.16	0.677
Observations	54		
R <sup>2</sup> / R <sup>2</sup> adjusted	0.005 / -0.034		

**Table B4:** Estimates from an LM model predicting the weight of *S. polaris* catkins per plot (square root g) with the number of catkins per plot. Residuals of this model has been used to create the catkin proxy. Include 95% confidence interval (CI) and p-value (p).

<i>Predictors</i>	<i>Estimates</i>	<b>Catkin weight per plot (sqrt of g)</b>	
		<i>95% CI</i>	<i>p</i>
(Intercept)	0.0589	0.0397 – 0.0780	<b>&lt;0.001</b>
number of catkins	0.0169	0.0139 – 0.0199	<b>&lt;0.001</b>
Observations	32		
R <sup>2</sup> / R <sup>2</sup> adjusted	0.814 / 0.808		

**Table B5:** Estimates of model output from an LM predicting the of *S. polaris* catkin proxy by leaves (square root g) and treatment. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing, Th = Thaw-freeze.

<i>Predictors</i>	<b>Catkin proxy</b>		
	<i>Estimates</i>	<i>95% CI</i>	<i>p</i>
(Intercept) [C]	0.05	0.01 – 0.09	<b>0.026</b>
leaves [sqrt]	-0.03	-0.07 – 0.01	0.093
treatment [I]	-0.01	-0.03 – 0.01	0.250
treatment [Th]	-0.04	-0.06 – -0.01	<b>0.004</b>
Observations	32		
R <sup>2</sup> / R <sup>2</sup> adjusted	0.299 / 0.224		

**Table B6:** Estimates from model output predicting length of *S. polaris* increments (log of mm) between 2019 and 2021, including only plots from the icing and controls groups. Predictors are treatment + year. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing.

<i>Predictors</i>	<b>Increment length (log)</b>		
	<i>Estimates</i>	<i>95% CI</i>	<i>p</i>
(Intercept)	1.69	1.58 – 1.80	<b>&lt;0.001</b>
treatment [I]	0.03	-0.12 – 0.19	0.677
year [2020]	-0.26	-0.39 – -0.14	<b>&lt;0.001</b>
year [2021]	-0.10	-0.22 – 0.03	0.132
<b>Random Effects</b>			
$\sigma^2$	0.07		
$\tau_{00 \text{ plot}}$	0.03		
ICC	0.34		
N <sub>plot</sub>	45		
Observations	105		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.103 / 0.405		

**Table B7:** Estimates from model output predicting number of *S. polaris* flowers per plot (log) between 2019 and 2021, including only plots from the icing and controls groups. Predictors are treatment + year. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing.

<i>Predictors</i>	<b>Flower number (log)</b>		
	<i>Log-Mean</i>	<i>95% CI</i>	<i>p</i>
(Intercept)	1.15	-0.45 – 2.75	0.158
plot mean of increment[log]	-0.29	-1.18 – 0.60	0.527
treatment[I]	0.08	-0.77 – 0.93	0.855
year[2020]	-0.42	-1.05 – 0.21	0.189
year[2021]	0.97	0.48 – 1.47	<b>&lt;0.001</b>
<b>Random Effects</b>			
$\sigma^2$	0.70		
$\tau_{00 \text{ plot}}$	1.33		
ICC	0.66		
$N_{\text{plot}}$	45		
Observations	105		
Marginal $R^2$ / Conditional $R^2$	0.130 / 0.701		



**Table B8:** Model estimates of the proportional apical shoot survival of *C. tetragona*. From a binomial GLMM and include shoots from the common garden and in-situ. Estimates have been back transformed by inverse logit. Predictors are year (2020 and 2021) + treatment. Random intercept is set at plot ID. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing, in-situ C = In-situ Control, in-situ C-P = potted in-situ Control.

<i>Predictors</i>	<b>Apical shoot</b>		
	<i>Odds ratio</i>	<i>95% CI</i>	<i>p</i>
(Intercept) [C]	0.58	0.24 – 0.86	0.675
year [2021]	0.06	0.02 – 0.15	<b>&lt;0.001</b>
treatment [I]	0.19	0.03 – 0.67	0.188
treatment [in-situ C]	0.98	0.84 – 1.00	<b>0.001</b>
treatment [in-situ C-P]	0.94	0.62 – 0.99	<b>0.017</b>
<b>Random Effects</b>			
$\sigma^2$	3.29		
T00 <sub>plot_id</sub>	2.43		
ICC	0.42		
N <sub>plot_id</sub>	22		
Observations	217		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.533 / 0.732		

**Table B9:** Model estimates of the proportional side shoot survival of *C. tetragona*. From a binomial GLMM and include shoots from the common garden and in-situ. Estimates have been back transformed by inverse logit. Predictors are year (2020 and 2021) × treatment as interactions. Random intercept is set at plot ID. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing, in-situ C = In-situ Control, in-situ C-P = potted in-situ Control.

<i>Predictors</i>	<b>Side-shoot</b>		
	<i>Odds ratio</i>	<i>95% CI</i>	<i>p</i>
(Intercept) [C]	0.90	0.81 – 0.95	<b>&lt;0.001</b>
year [2020]	0.34	0.19 – 0.52	0.087
year [2021]	0.09	0.04 – 0.17	<b>&lt;0.001</b>
treatment [I]	0.51	0.26 – 0.76	0.916
treatment [in-situ C]	0.82	0.46 – 0.96	0.073
treatment [in-situ C-P]	0.40	0.17 – 0.67	0.462
year [2020] * treatment [I]	0.26	0.11 – 0.50	<b>0.048</b>
year [2021] * treatment [I]	0.20	0.08 – 0.42	<b>0.011</b>
year [2020] * treatment [in-situ C]	0.46	0.12 – 0.85	0.868
year [2021] * treatment [in-situ C]	0.81	0.40 – 0.96	0.129
year [2020] * treatment [in-situ C-P]	0.48	0.23 – 0.73	0.857
year [2021] * treatment [in-situ C-P]	0.82	0.61 – 0.93	<b>0.005</b>
<b>Random Effects</b>			
$\sigma^2$	3.29		
T00 <sub>plot_id</sub>	0.38		
ICC	0.10		
N <sub>plot_id</sub>	22		
Observations	326		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.340 / 0.408		

**Table B9:** Model estimates of the proportional juvenile side-shoot survival of *C. tetragona*. From a binomial GLMM and include shoots from the common garden and in-situ. Estimates have been back transformed by inverse logit. Predictors are year (2020 and 2021) + treatment. Random intercept is set as plot ID. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing, in-situ C = In-situ Control, in-situ C-P = potted in-situ Control.

<b>Juvenile side-shoots</b>			
<i>Predictors</i>	<i>Odds ratio</i>	<i>95% CI</i>	<i>p</i>
(Intercept) [C]	0.99	0.92 – 1.00	<b>&lt;0.001</b>
year [2020]	0.31	0.08 – 0.69	0.321
year [2021]	0.08	0.02 – 0.27	<b>0.001</b>
treatment [I]	0.11	0.03 – 0.35	<b>0.005</b>
treatment [in-situ C]	0.72	0.29 – 0.94	0.309
treatment [in-situ C-P]	0.46	0.15 – 0.81	0.858
<b>Random Effects</b>			
$\sigma^2$	3.29		
T00 <sub>plot_id</sub>	0.95		
ICC	0.22		
N <sub>plot_id</sub>	22		
Observations	327		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.351	0.496	

**Table B10:** Model estimates of the number of juvenile shoots per individual *C. tetragona* on original log-scale. From a GLMM with log link and poisson distribution. It includes shoots from the common garden and in-situ.. Predictors are year (2020 and 2021) + treatment. Random intercept is set as plot ID. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing, in-situ C = In-situ Control, in-situ C-P = potted in-situ Control.

<i>Predictors</i>	<b>Juvenile side-shoots</b>		
	<i>Log-Mean</i>	<i>95% CI</i>	<i>p</i>
(Intercept) [C]	-0.97	-1.51 – -0.44	< <b>0.001</b>
year [2020]	0.68	0.38 – 0.99	< <b>0.001</b>
year [2021]	1.26	0.97 – 1.54	< <b>0.001</b>
treatment [I]	0.11	-0.57 – 0.79	0.757
treatment [in-situ C]	0.30	-0.41 – 1.00	0.406
treatment [in-situ C-P]	0.52	-0.18 – 1.22	0.149
<b>Random Effects</b>			
$\sigma^2$	0.69		
$\tau_{00}$ plot_id	0.28		
ICC	0.29		
$N_{\text{plot\_id}}$	22		
Observations	327		
Marginal $R^2$ / Conditional $R^2$	0.2390.460		

**Table B11:** Model estimates of the number *C. tetragona* flowers per plot on original log-scale. From a GLMM with log link and poisson distribution. It includes shoots from the common garden and in-situ. Predictors are year (2020 and 2021) + treatment. Random intercept is set as plot ID. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing, in-situ C = In-situ Control, in-situ C-P = potted in-situ Control.

<i>Predictors</i>	<b>Flower number (log)</b>		
	<i>Log-Mean</i>	<i>CI</i>	<i>p</i>
(Intercept)	2.90	2.29 – 3.51	<b>&lt;0.001</b>
treatment [I]	-2.56	-3.58 – -1.55	<b>&lt;0.001</b>
treatment [in-situ C]	1.47	0.58 – 2.36	<b>0.001</b>
treatment [in-situ C-P]	0.12	-0.78 – 1.03	0.794
year [2021]	-1.18	-1.33 – -1.03	<b>&lt;0.001</b>
<b>Random Effects</b>			
$\sigma^2$	0.11		
T00 <i>plot_id</i>	0.53		
ICC	0.83		
N <i>plot_id</i>	22		
Observations	44		
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.801 / 0.966		

**Table B12:** Model estimates of the number *C. tetragona* flowers in 2020 per plot on original log-scale. The proportion of alive shoots + treatment. Random intercept is set as plot ID. GLMM with log link and poisson distribution is used. It includes shoots from the common garden. Include 95% confidence interval (CI) and p-value (p). C = Control, I = Icing, in-situ C = In-situ Control, in-situ C-P = potted in-situ Control.

<i>Predictors</i>	<b>Flower number in 2020 (log)</b>		
	<i>Log-Mean</i>	<i>CI</i>	<i>p</i>
(Intercept)	3.09	2.47 – 3.77	<b>&lt;0.001</b>
Proportion of alive shoots	0.28	-0.50 – 1.03	0.444
treatment [I]	-2.42	-2.91 – -1.94	<b>&lt;0.001</b>
Observations	59		
R <sup>2</sup> Nagelkerke	0.859		

