

Norwegian University
of Life Sciences

Master's Thesis 2023 30 ECTS

The Faculty of Environmental Sciences and Natural Resource Management

Experimentally testing the effect of increased temperature on senescence rate of three plant species utilized by the Svalbard reindeer

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Preface

This master's thesis is the final part of my two-year master's degree in Natural Resource Management at the faculty of Environmental Sciences and Natural Resource Management at the Norwegian University of Life Sciences (NMBU).

I would like to thank my supervisor, Professor Leif Egil Loe, for his guidance throughout my thesis, as well as for the opportunity to take part in this project and conduct fieldwork on Svalbard. I would also like to thank my co-supervisors, PhD student Samantha Dwinnell and Professor René van der Wal, for their help and input both during fieldwork and writing. Your knowledge and enthusiasm for this project has been an inspiration.

Finally, I would like to thank my friend and study partner, Emilie Kvåle Sletterød Andersen, for her help and support throughout the whole thesis process. I couldn't have done it without you!

Norwegian University of Life Science

Ås, May 2023

A handwritten signature in cursive script, reading "Caroline Iveland". The signature is written in black ink and is positioned above a horizontal line.

Caroline Iveland

Abstract

The Arctic is experiencing the most rapid climate warming on earth. While the climate induced changes in spring have received a lot of attention, similar studies for the effects in autumn have been neglected. In this thesis I experimentally investigate the effects that elevated temperatures and moisture levels in summer may have on the senescence rate of three of the most common foraging plants of the Svalbard reindeer. Open top chambers and heating ovens were used to manipulate the temperature and additional water was given to manipulate the soil moisture. I found that increased temperatures had a positive effect on all three species, while moisture only influenced *Salix polaris*. Onset of senescence was delayed for *Alopecurus ovatus* and *Bistorta vivipara*, and the rate of senescence was slowed for *S. polaris* and *B. vivipara*. The prolonged autumn with a greater amount of plant biomass could counteract the negative effects of harsh winters on the body mass of the Svalbard reindeer, and result in population growth. Thus, the future of the Svalbard reindeer and its foraging plants may be brighter than previously expected.

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1. Introduction

Climate change is causing a worldwide rise in temperature, and in the Arctic the annual mean surface temperature is rising at a rate three times higher than that of the global average (Adakudlu et al., 2019; AMAP, 2021). These changes can lead to alterations in the tundra plant phenology with implications for plant pollinator interactions, productivity, carbon and energy balances, seasonality, distribution, and herbivory (AMAP, 2021; Beard et al., 2019). The Arctic tundra is among the least studied biomes in response to climate induced changes (Diepstraten et al., 2018), and it is therefore crucial to improve our understanding of how elevated temperatures influence the terrestrial ecosystem in Svalbard, and hence what consequences such changes will have on its herbivores.

Plants have a central role in the flow of energy and nutrients through food webs (Van der Wal & Stien, 2014), and studies show that there have been changes in both their productivity and vegetation composition in response to climate change (Kapfer et al., 2017). Understanding the sensitivity of the plants is critical to forecast the future vegetation composition and feedbacks to the climate (Elmendorf et al., 2012). Several satellite-based studies are reporting a general greening of Svalbard, but very few ground-based studies have been carried out to confirm this change (Callaghan et al., 2011; Epstein et al., 2012). Satellite-based studies are not able to pick up on separations of productivity between vascular plants and mosses, nor detect plant community changes beyond the level of tall shrub encroachment due to the low spatial resolution of the satellite imagery (Van der Wal & Stien, 2014), and more ground-based studies are needed to understand such changes and the interactions connected to them.

Phenological changes in plants that are driven by climate change, particularly during springtime, have received a lot of attention due to the high incidence of asynchrony across the different trophic levels (Kharouba et al., 2018), mismatches that may occur with consequences on both a populational and evolutionary level (Visser & Gienapp, 2019), and potentially disrupt the function, persistence, and resilience of the ecosystem (Thackeray et al., 2010). However, similar studies concerning how warming influences the timing of plant phenophases, such as senescence, particularly later in the season remain few and far between (Gallinat et al., 2015), despite the potential importance to the ecosystem (Piao et al., 2019). This calls for further studies into the changes during autumn and their importance.

The seasons are changing differently in response to climate change, and they are also affecting each other. The summer season has been prolonged (Serreze et al., 2009), which has led to an increased heat flux in the autumn and early wintertime (Vihma, 2014). There are also higher temperatures in late winter and spring that have led to earlier snowmelt in some regions (McBean et al., 2005; Raisanen, 2008) with a possible effect on the timing of bud burst and a shift in the end of the growing season for the plants (Semenchuk et al., 2016). Due to the short growing season, a late timing of senescence is important to maximize the growth period, reproduction, and to allow enough time to develop frost hardiness and nutrient resorption for plants in the Arctic (May & Killingbeck, 1992). It is still uncertain what drives the onset and rate of senescence (Gehrmann et al., 2021; Livensperger et al., 2019), but the onset of senescence in Arctic plants have been found to advance with higher spring and summer temperatures, suggesting that it could be controlled by the growing season temperatures (Oberbauer et al., 2013). Collins et al. (2021) supported this hypothesis as they found a delay in leaf senescence of 0.8 days in response to warming (0.5-2.3°C), and a lengthening of the growing season both during spring and autumn with a consistent pattern across sites, species, and over time. The rate of senescence has also been found to slow with warming (Estiarte & Peñuelas, 2015; May et al., 2017).

Elevated temperatures in the summer season has also been found to stimulate plant productivity across many arctic tundra biomes (Berner et al., 2020). Supporting this, Van der Wal & Stien (2014) found a positive relationship between summer temperatures and plant biomass across habitats, plant functional types, and species, and they determined that the summer weather conditions were the key driver behind this plant productivity. Kapfer et al. (2017) also found that the warming had contributed to significant changes in the plant communities. However, other factors, in addition to temperature, may cause changes in the plant composition. Increased precipitation is argued to compensate for the potential drying out of the soil owing to the warmer temperatures caused by climate change, at least to a certain extent (Engler et al., 2011). Still, increased summer precipitation has only been found to produce a few responses in Arctic plants compared to other environmental variables (Phoenix et al., 2001).

Svalbard Airport has experienced an increase in the mean annual temperature of 3.7°C over the past 118 years, equaling about three times as much as the global warming for the same period. It is expected that there will be an increase in the annual mean temperature of about

3°C, 6°C, and 10°C for the emission scenarios RCP2.6, RCP4.5, and RCP8.5, respectively, over the next 80 years (Adakudlu et al., 2019). The higher temperatures will help drive the Arctic water cycle in the future, and there has been estimated a 10% increase in annual rainfall at Svalbard Airport, and an increase of more than 20% during the autumn and winter time (Adakudlu et al., 2019; Førland et al., 2011).

The interaction between the Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its feeding plants is one interaction that is likely to be affected by climate change. The Svalbard reindeer is a key species to the structure and functioning of the tundra food web as it is the only large herbivore in the high Arctic Svalbard archipelago (Van Der Wal, 2019). It is endemic to Svalbard and the population size was estimated to be approximately 22-22 500 individuals in 2019 (Le Moullec et al., 2019; Van Der Wal, 2019). The population size is currently still rising after a protection was placed on the species in 1925, but also due to the loss of ice and re-establishing after the heavy hunting by humans in earlier years (Le Moullec et al., 2019). Despite these positive indications, there are still some uncertainties surrounding how climate change will affect them through events such as “rain-on-snow” (ROS) that may encase their winter forage in ice (Putkonen & Roe, 2003; Rennert et al., 2009), and also how they will indirectly be affected through changes in their foraging plants during the snow free periods of the year in the future.

The Svalbard reindeer eat vascular plants, mosses, and lichen (Bjørkvoll et al., 2009; Joo et al., 2014; Staaland et al., 1993; Van der Wal et al., 2000; Åhman & White, 2018), but their diet changes with the seasonal availability of their foraging plants (Bjørkvoll et al., 2009). During the summer, graminoids, forbs and dwarf shrubs dominate their diet (Bjørkvoll et al., 2009; Åhman & White, 2018). Three of their most favored foraging plants are the grass species polar foxtail (*Alopecurus ovatus*), the shrub species polar willow (*Salix polaris*), and the forb alpine bistort (*Bistorta vivipara*) (Bjørkvoll et al., 2009; Joo et al., 2014). All three species are common throughout Svalbard and are abundant in the study area (Rønning, 1996; Tømmervik et al., 2014).

In this thesis, I will investigate the effects that elevated summer temperatures and soil moisture level will have on the three study species *A. ovatus*, *S. Polar*, and *B. vivipara* using a replicated full factorial experiment with three heating levels and two moisture levels. It is important to study the changes in the terrestrial ecosystem in Svalbard to understand the

future changes in different food webs, here with an emphasis on the interaction between the Svalbard reindeer and three of its foraging plants. Specifically, my thesis will examine if elevated temperatures and soil moisture levels can delay the onset of senescence and slow the rate of senescence for the three study species.

2. Method

2.1 Study area

The study was carried out in Adventdalen ($78^{\circ}N$, $15^{\circ}E$), Svalbard (fig. 1). Adventdalen is a large trough valley surrounded by steep mountains and glaciers with a few side valleys. The area around the river Adventelva has become a large, important wetland area (Barr, 2021).

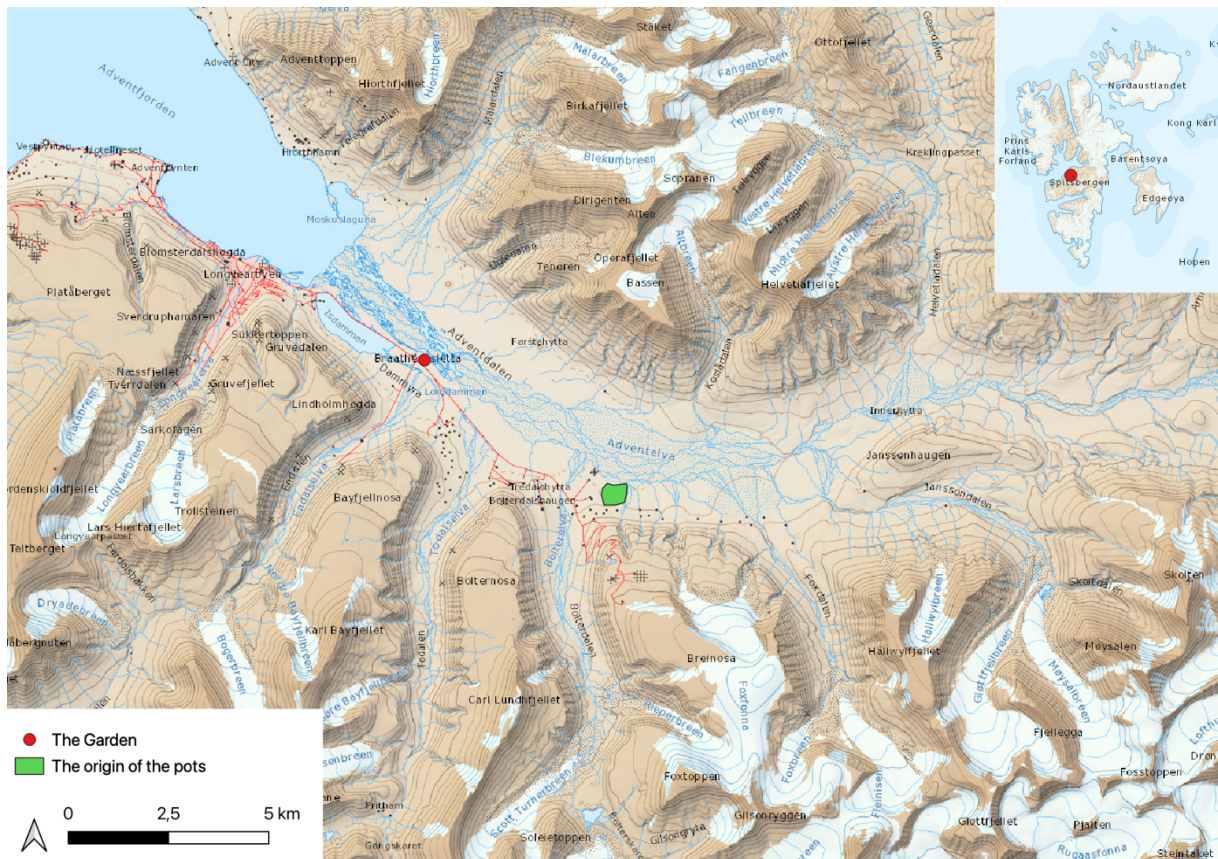


Figure 1 Adventdalen. The red dot marks the location of the garden, and the green polygon marks the area where samples in the pots were collected. The map in the upper righthand corner shows the location of Adventdalen in Svalbard. The map data was provided by the Norwegian Polar Institute (Norwegian Polar Institute, 2020) and the map was made using QGIS (vers. 3.16.11-Hannover).

Adventdalen is characterized by a dry Arctic climate, and has a nutrient rich soil (Johansen et al., 2012). The vegetation in the lower flat areas are dominated by bryophyte-rich fens and

marches, while the more elevated, exposed and dryer areas have plant communities dominated by *S. polaris*, *Cassiope tetragona*, or *Dryas octopetala* (Tømmervik et al., 2014).

The temperature in Adventdalen ranges from an average of 7°C in July, the warmest month, to an average of -11°C in March, the coldest month, and the yearly amount of precipitation is at 221.5 mm per year (timeanddate.no, n.d.). During the study period in 2022 the average temperature was 9.3°C, 6.9°C, and 3.2°C with a total of 5.1 mm, 41.5 mm, and 26.7 mm precipitation in July, August, and September respectively. July was warmer and dryer than normal, August was warmer and wetter, and September was warmer than usual, but had a normal amount of precipitation (yr.no, n.d.). There was no snow in July and August, but in September there was a thin and occasionally patchy snow cover between the 13th and the 22nd.

2.2 Study Species

Among the three species that have been studied there is one grass species, one forb species, and one shrub species, and they are all abundant species in Adventdalen (Rønning, 1996).

The polar foxtail (*Alopecurus ovatus*, previously *Alopecurus borealis*) is a very long-lived, perennial grass with a 1-flowered spikelet that belongs to the Poaceae family. It is a graminoid herb that often grows in extensive mats due to their horizontal, branched rhizomes. The roots run relatively deep into the ground. Each stem is solitary and can reach on average between 7-25 cm. The leaves are flat, tapered along their length, rough on the upper side with distinctly raised lateral veins, and have a green to green-grey color. The inflorescence is a short, compact, and oblong. It occupies less than 1/5 to 1/10 of the culms with numerous nodes and branches at each node. The color is hidden by dense silky white hairs throughout, but at the beginning of the flowering season it can have an intense red color. The sexual reproduction happens through seeds that get dispersed by the wind or animals, but locally it can reproduce by clonal growth from its rhizomes. It grows in moist places and usually on fine-grained substrates such as close to rivers, small lakes, meadows, shallow mires, sediment plains, moss tundra and at the foot of bird cliffs (Alsos et al., n.d.; Rønning, 1996).

The polar willow (*Salix polaris*) is a potentially very long-lived, perennial wood that belongs to the Salicaceae family. It is a low mat-forming prostrate dwarf shrub with extensive branched subterranean stems that can form stands of 1 m² or larger. It has shoots with leaves

at soil level that reach an average of 1-3 cm. The leaves are oval with not conspicuous pinnate veins that do not reach the margin, it has entire margins, and both surfaces are dark green and glossy. The inflorescences are dense, pedunculate, many-flowered spikes that appear at the same time as the leaves. The plants are unisexual and sexual reproduction happens through seeds. Pollination happens by wind, but probably also by insects, and dispersal happens through wind and partly by attaching to animals. It is common in heaths, slopes, snowbeds, patterned ground and nearly all kinds of open ground, and it can also grow in large, highly branching stands on gravel. The substrate it can grow on ranges from mixed to fine textures with good to poor drainage (Alsos et al., n.d.; Rønning, 1996).

The alpine bistort (*Bistorta vivipara*) is a moderately long-lived, perennial knotweed that belongs to the Polygonaceae family. It is a solitary herb with a short, thick rhizome that is often curved upwards at the apex. The shoots reach an average of 3-10 cm. The leaf is oblong, has a mid-vein that is raised on the lower surface, the upper surface is dark green or reddish and smooth, the lower surface is pale green. The inflorescence is spike-like with white or pink flowers. Vegetative reproduction happens through bulbils and dispersal by water, mammals, and birds. It can grow on almost any substrate from heaths to shallow mires and sediment plains, from dry to moist ground and is often abundant (Alsos et al., n.d.; Rønning, 1996).

2.3 Experimental study design

The garden was established at the old northern lights station ($78^{\circ}12'N$, $15^{\circ}49'E$) in Adventdalen and the vegetation used in the experiment was collected from an area between the foot of Breinosa and Adventelva ($78^{\circ}10'N$, $16^{\circ}01'E$) (fig. 1). The vegetation where the vegetation columns were collected was typical for the more elevated, exposed and dryer sites in the valley with plant communities dominated by *S. polaris*, *Cassiope tetragona*, or *Dryas octopetala* (Tømmervik et al., 2014).

A pot consisted of an approximately 25 cm long pipe with a diameter of 20 cm with a column of vegetation inside. The vegetation columns were approximately 20 cm long. To control the drainage 2 sheets of garden cloth were placed over the bottom of the pipes for those that would receive the dry treatment and 3 sheets over those that would receive the wet treatment. Each pot was given 0.5L of water twice a week (Tuesdays and Fridays) to be kept alive before the experiment started. The amount was raised to 1L each for the pots that received the wet

treatment while the dry continued to receive 0.5L of water each after the experiment started on the 2nd of august. The watering regime was continued until the end of the experiment with the final watering on the 20th of September.

There were 30 pots in total that were split into 5 blocks in the garden (fig. 2). Two of the blocks (block 3 and 5) had pots from the previous year (2021) while the three remaining were made with new pots. Pots were placed in pairs in each open top chamber (OTC) where one received the dry treatment and the other received the wet treatment (fig. 3). Three OTCs would then make up one block where one of the OTCs would have 6 heating ovens, the other would have 3 heating ovens, and the final one would be the control without any heating ovens. Additionally, each pot had one TOMST TMS-4 datalogger within it that measured the temperature at approximately 6 cm into the soil, at ground level, and in the air at approximately 15 cm above the ground, as well as the soil moisture level. It uses the time-domain transmission (TDT) method to measure the soil moisture (Wild et al., 2019). It is normal to calibrate the TDT raw data into volumetric soil moisture, however this was not within the scope of this thesis. The TOMST was removed for the period it took to take the measurements each time, and these periods have been excluded from the data that has been used.

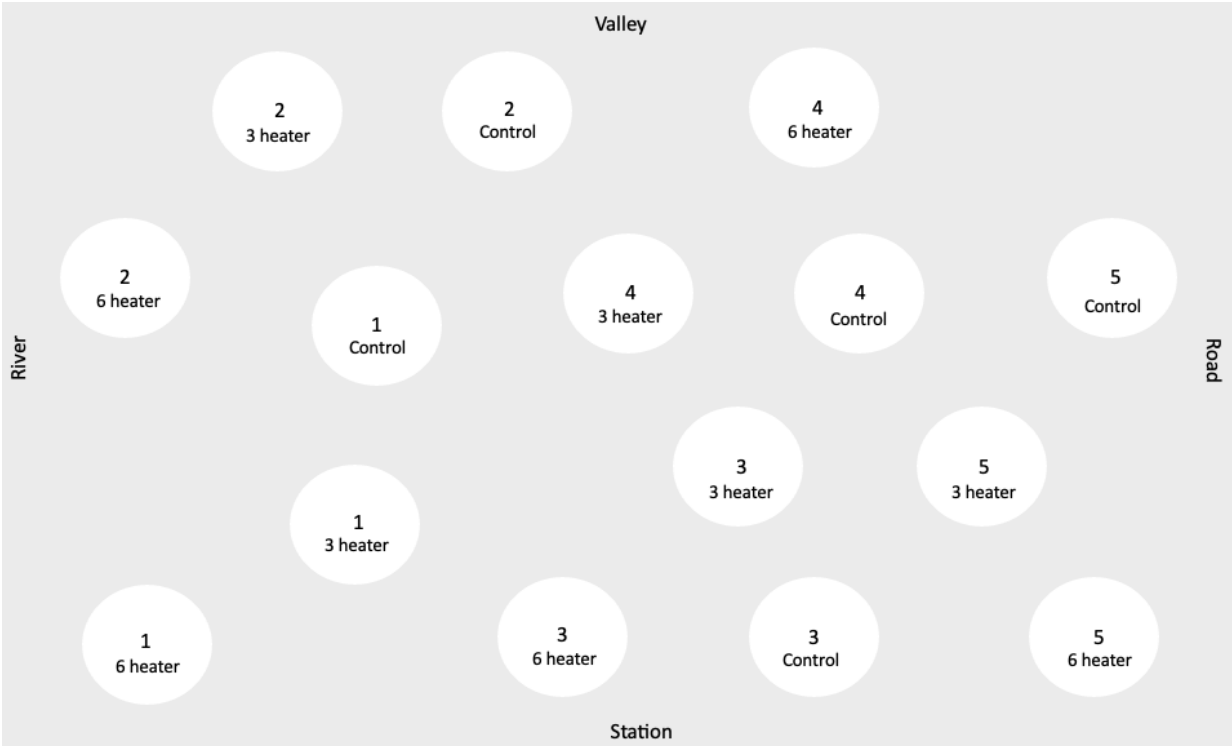


Figure 2 Garden layout. Each circle represents an OTC where the number indicates which block it belongs to, and the heat treatment is noted below the block number.

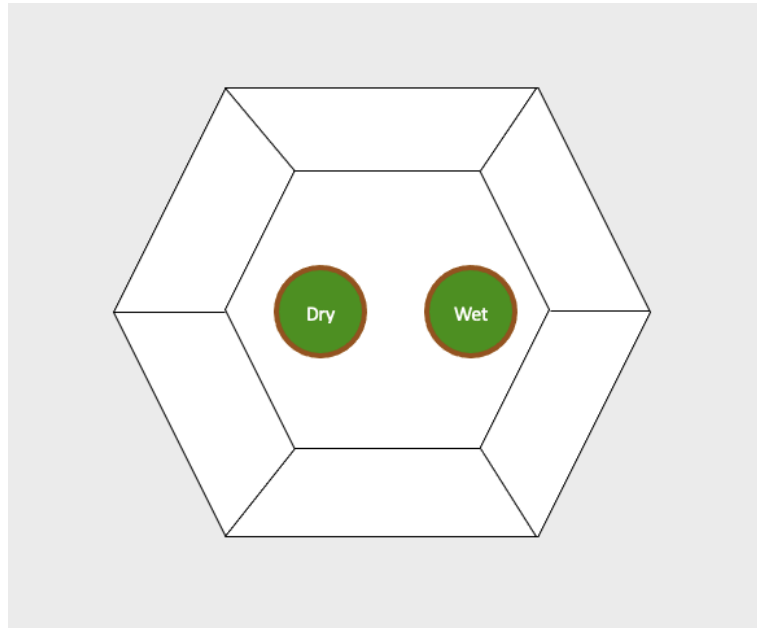


Figure 3 OTC layout. The green circles represent the pots, with moisture treatment, within each OTC.

Plots for the pots had to include at least one representative of each of the three species, and these had to be further than within 5 cm from the edge so that the root systems would not be too damaged. The vegetation columns were then dug up, placed inside the pipes, the pipes filled with soil until they were entirely packed, the underside was covered with garden cloth, and then placed back inside the ground for the vegetation to settle in the pipes. The pots were moved to the garden after a week and were given another week to settle in the new environment. This was necessary as the garden itself consisted of only sand and smaller rocks with no soil available to the pots. Geotextile was also placed all around the pots to prevent sand from being blown into them. The pots from last year simply remained as they were in the garden.

Heating was applied between the 2nd of August and the 29th of August 2022, while the watering regime was continued until the 20th of September 2022. The goal was to start with the different treatments before senescence had started within any of the three study species and keep them throughout their senescence until death or total snow cover. Measurements were taken until the 22nd of September 2022 to capture the effect of the treatments post heating as well.

2.4 Data collection

The data was collected in the period between the 20th of July and the 22nd of September. Measurements were taken from each block throughout the week so that there would be approximately a week's time between each measurement taken in the specific blocks.

For each pot and measurement date, the following data on *A. ovatus* were recorded: block, heat treatment, water regime, shoot id, leaf id, presence or absence of inflorescence, length of leaf (including inflorescence if present), percentage green closest to the nearest 5 out of a hundred, if the individual was a new shoot, or any other additional comment about the leaf noted. The shoot and leaf id within a pot could differ between each week as it was the pots that were followed and not the specific individuals within them. The individuals were measured as long as at least one leaf was 5% or more green. To study the same area within the pots each time a circular grid was used. It had a diameter of 10 cm and was equipped with sticks on the outer side so that it would be "locked" at the same place within the pot. For *A. ovatus*, nine of the pots had too great a number of individuals for the registration to be feasible and it was decided that the grid would be split in half, using a string, in these pots. The half was selected by random and marked in order to always measure the same half.

For each measurement of *S. polaris* and *B. vivipara* the date, block, heat treatment, water regime, pot id, color of each single leaf (green, yellow, red, or brown), presence or absence of inflorescence, or any other additional comment about the individual was noted. The entire pot was measured for *S. polaris* and *B. vivipara* and the individuals were documented as long as they remained attached to the ground.

In addition, 59 shoots were collected to find the biomass for *A. ovatus*. The length of each leaf of an individual was measured and summarized to gain the total length of the shoot before they were dried and measured to obtain the weight of each shoot. In the end, total length and weight of each shoot was multiplied to get the biomass.

At the end of the experiment all equipment, except from the pots in the garden, was removed and brought back for storage or recycling. The pots were left for future experiments.

2.5 Data handling

The data was curated using the R-package tidyverse (Wickham et al., 2019) and made ready for analyses.

The methodology changed for *A. ovatus* after the first week, as width measurements of each shoot was dropped due to time constraints and the first week has therefore been excluded from the dataset.

2.6 Statistical analyses

All of the statistical analysis was performed in RStudio version 2022.12.0+353 (RStudioTeam, 2021).

To analyze the effect of raised temperatures I used generalized linear mixed effects model (GLMM) with the glmer function. Count of green leaves was used as a response variable for all three species, and the family argument was set to “poisson”. Heat treatment, water regime, and week was used as explanatory variables for all three study species, as well as all interactions up to the third order for *A. ovatus* and the second order for *S. polaris* and *B. vivipara*. The pot’s ID was used as random effect and the initial number of green leaves per pot was used as offset variable. Likelihood Ratio Test (LRT; using the anova function) (Pinheiro & Bates, 2000) was used to find the best model. When an interaction fell out, the least significant of the main effects of heat treatment, water regime and week was attempted removed until all remaining predictor variables were significant. Bootstrapping was used as a final model to create confidence intervals around predicted effect sizes in the final model.

For *A. ovatus* I measured and weighted shoots, allowing me to estimate the change in green biomass over time. In addition to using the final count of green shoots model, described above, I also fitted a model for the total leaf length of a shoot being green. For this I used a linear mixed effects model (lmer) fitted with the function of the same name, using the summed length of the green parts of all leaves on a shoot as response variable. This variable was log-transformed to reduce heteroskedasticity of residuals. Errors were assumed to be normally distributed. Fixed and random effects and model selection approach was similar to the model above. The predicted length of green leaves was converted to dry biomass through the known relationship between length of shoots and mass (see appendix). Finally, because

count of green leaves decreased from summer to autumn (as they senesced), mass was multiplied with the predicted count of remaining leaves, to provide an estimate of change in total biomass over time.

3. Results

3.1 Temperature and moisture data

The average temperature in the soil had approximately a 0.6°C and 0.9°C difference, 1°C and 2.1°C difference at the ground level, and 1.2°C and 2.1°C difference in the air between the control and the 3 heater and the 6 heater, respectively (fig. 4). The largest differences in heat between the control and a treatment can be found in the air and the smallest difference is found in the ground, suggesting that the soil does not retain the heat as well as the air does when the same amount of heat is applied. There is a general decrease in the temperature independently of the heat treatments, control included, due to the approaching winter.

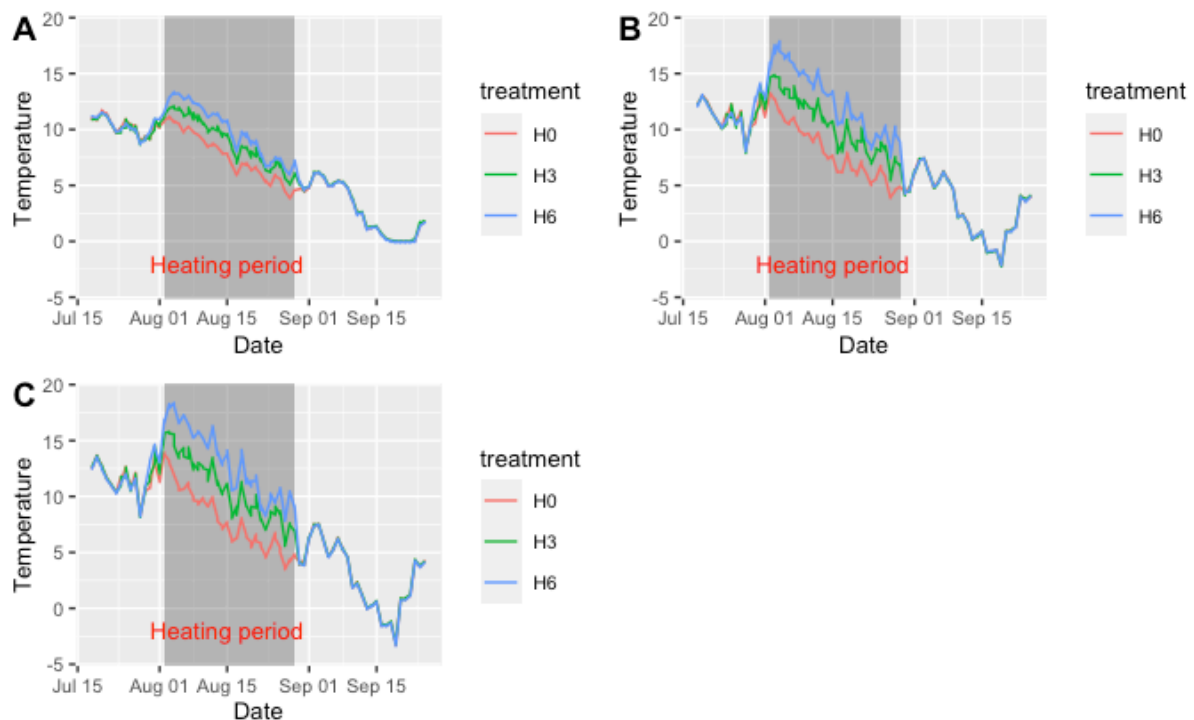


Figure 4 The red lines show the change in the different temperatures (°C) that had 0 heaters over the study period, the green lines show the same for the pots that had 3 heaters, and the blue lines for the pots that had 6 heaters. Figure A show the soil temperature, figure B show the ground level temperature, and figure C show the air temperature.

There is a clear difference between the two moisture treatments where the dry is dryer than the wet treatment (fig. 5). The average mean relative moisture in raw TDT data for the dry

treatment is 1663, 1686 and 1661 for the control, the 3 heater, and the 6 heater, respectively. For the wet treatment it is 1935, 1823 and 1825 for the control, the 3 heater, and the 6 heater, respectively. The difference between the two treatments is approximate 570. Peaks are generally a result of watering, but they can also be a result of heavy rain such as the peak on the 19th of August where it rained 16.9 mm that day. The drop in the second half of September is due to freezing during a snow fall that lasted for approximately a week to a week and a half (yr.no, n.d.).

The dry treatment has a less clear pattern in which of the heat treatments and the control that are the driest and wettest (fig. 5). Pre heating the 3 heater is generally the driest and the 6 heater the wettest, but the control and the 3 heater switch during the heating period until the heavy rainfall on the 19th of August where the 3 heater again returns to being the driest out of the two heat treatments and the control. There is a new heavy rainfall (10.9 mm) on the 10th of September (yr.no, n.d.), and following this the 3 heater becomes the driest out of the two heat treatments and the control. While for the wet treatment the control is the wettest and the 6 heater is the driest out of the two heat treatments and the control. The heating can have dried out the surface and hence explain this pattern. The freezing during the snow cover brings the two heat treatments and the control to the approximately same level of soil moisture. Additionally, during the heavy rainfall on the 19th of August both heat treatments and the control reach approximately the same level of saturation, suggesting that the soil in the pots might have reached its max saturation level.

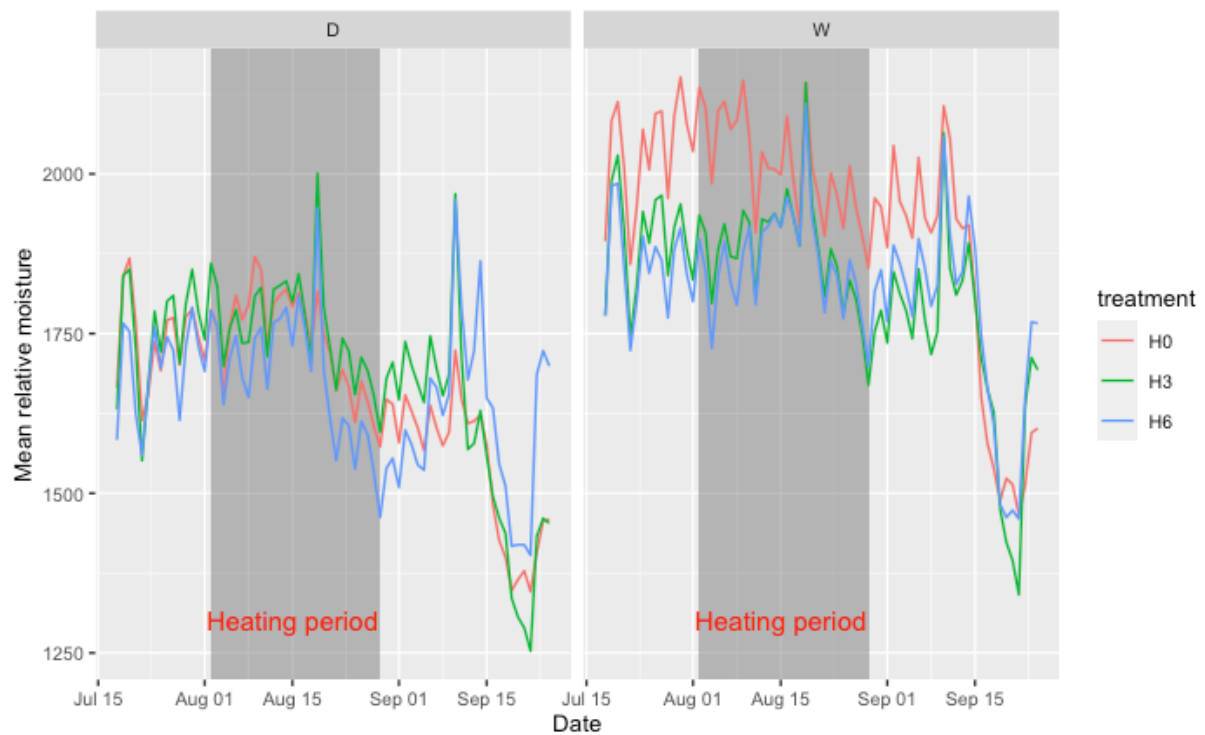


Figure 5 The left figure (D) shows the change in the mean relative moisture level for the pots that received the dry treatment, and the right figure (W) shows the same for those pots that received the wet treatment. The red lines show the change in the mean relative moisture level for the pots that had 0 heaters over the study period, the green lines show the same for the pots that had 3 heaters, and the blues line for the pots that had 6 heaters.

3.2 *A. ovatus*

The final model for count of green leaves included only the effect of week, with both treatment effects including interactions falling out of the model, with the counts dropping substantially only in the last two weeks of the study (table 1). In contrast, the total length of green leaves responded to heat treatment, but not moisture treatment as the final model retained the effect of week, heat treatment and two way interaction (table 2).

Table 1 The effect of week on the number of live shoots of *A. ovatus*. The number of live shoots were unaffected by the heat or moisture treatments.

| Random effects: | | | | |
|---|-----------|----------|----------|---|
| Groups | Name | Variance | Std.Dev. | |
| Pot ID | Intercept | 0.01 | 0.10 | |
| Number of obs.: 270, groups: pot ID, 30 | | | | |
| Fixed effects: | | | | |
| | Estimate | SE | z | P |

| | | | | |
|------------------|--------|------|-------|--------|
| Intercept | <0.001 | 0.04 | -0.01 | 0.99 |
| Week 31 | 0.02 | 0.05 | 0.44 | 0.66 |
| Week 32 | <0.001 | 0.05 | 0 | 1.00 |
| Week 33 | 0.03 | 0.05 | 0.49 | 0.62 |
| Week 34 | 0.06 | 0.05 | 1.08 | 0.28 |
| Week 35 | 0.05 | 0.05 | 1.05 | 0.29 |
| Week 36 | 0.01 | 0.05 | 0.23 | 0.82 |
| Week 37 | -0.28 | 0.06 | -5.06 | <0.001 |
| Week 38 | -0.20 | 0.05 | -3.62 | <0.001 |

Table 2 The interacting effect of heat treatment and week on length of green leaves of *A. ovatus*.

| Random effects: | | | |
|---|------------------|-----------------|-----------------|
| Groups | Name | Variance | Std.Dev. |
| Pot ID | Intercept | 0.08 | 0.28 |
| Residual | | 0.57 | 0.75 |
| Number of obs.: 6490, groups: pot ID, 30 | | | |
| Fixed effects: | | | |
| | Estimate | SE | t |
| Intercept | 4.2 | 0.10 | 42 |
| Treatment (H3 vs. C) | 0.03 | 0.14 | 0.19 |
| Treatment (H6 vs. C) | 0.03 | 0.14 | 0.18 |
| Week 31 | 0.04 | 0.07 | 0.51 |
| Week 32 | -0.01 | 0.07 | -0.21 |
| Week 33 | -0.09 | 0.07 | -1.4 |
| Week 34 | -0.27 | 0.07 | -4.0 |
| Week 35 | -0.56 | 0.07 | -8.3 |
| Week 36 | -0.82 | 0.07 | -12 |
| Week 37 | -0.69 | 0.08 | -9.0 |
| Week 38 | -1.50 | 0.07 | -21 |
| Treatment (H3 vs. C) x Week 31 | -0.15 | 0.10 | -1.6 |
| Treatment (H6 vs. C) x Week 31 | -0.04 | 0.10 | -0.41 |
| Treatment (H3 vs. C) x Week 32 | -0.02 | 0.10 | -0.19 |
| Treatment (H6 vs. C) x Week 32 | -0.08 | 0.10 | -0.82 |
| Treatment (H3 vs. C) x Week 33 | 0.04 | 0.10 | 0.38 |
| Treatment (H6 vs. C) x Week 33 | -0.02 | 0.10 | -0.22 |
| Treatment (H3 vs. C) x Week 34 | 0.16 | 0.10 | 1.6 |
| Treatment (H6 vs. C) x Week 34 | 0.11 | 0.09 | 1.2 |

| | | | |
|---------------------------------------|------|------|-----|
| Treatment (H3 vs. C) x Week 35 | 0.24 | 0.10 | 2.5 |
| Treatment (H6 vs. C) x Week 35 | 0.38 | 0.09 | 4.0 |
| Treatment (H3 vs. C) x Week 36 | 0.19 | 0.10 | 2.0 |
| Treatment (H6 vs. C) x Week 36 | 0.41 | 0.10 | 4.3 |
| Treatment (H3 vs. C) x Week 37 | 0.11 | 0.11 | 1.0 |
| Treatment (H6 vs. C) x Week 37 | 0.26 | 0.10 | 2.4 |
| Treatment (H3 vs. C) x Week 38 | 0.43 | 0.10 | 4.2 |
| Treatment (H6 vs. C) x Week 38 | 0.55 | 0.10 | 5.5 |

In combination, the decrease in counts of green leaves over time (table 1) and the temperature dependent decrease in the length of green leaves (table 2), produced a pronounced effect on green biomass. There was a decrease in green biomass for both heating treatments and the control throughout the study period (fig. 6). However, the decrease goes slower for both the 3 heater and the 6 heater from approximately a week after the heating period started. The decrease almost stops for the 6 heater for as long as the heating is implemented but falls at a similar rate to the control in September. The 3 heater has a similar pattern to the 6 heater, but the decrease in green biomass starts about a week earlier. There is a slight suggestion to an interaction during the heating period, but no interaction for either of the treatments after the heating was stopped. The effect of heating is only additive after the heating period, but the effect can be seen for the next few weeks.

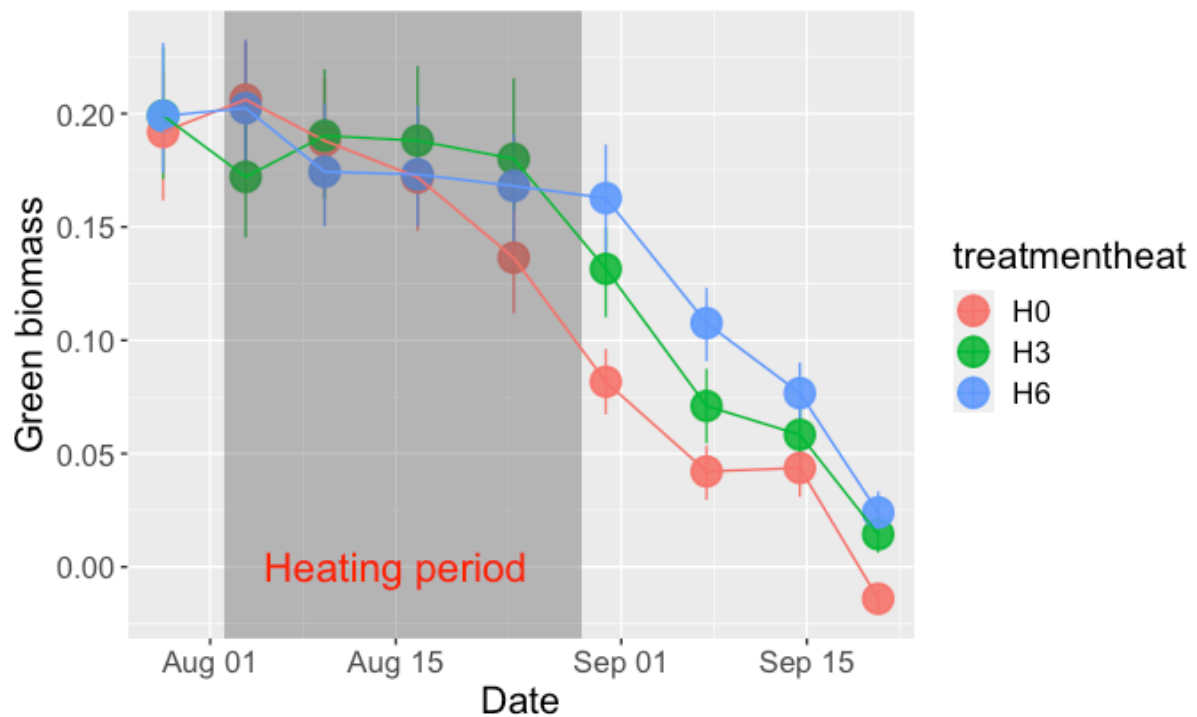


Figure 6 Effect of early heating on *A. ovatus*. The red line shows the change in the green biomass for the pots that had 0 heaters over the study period, the green line shows the same for the pots that had 3 heaters, and the blue line for the pots that had 6 heaters. The shaded area shows the period for when the heating was applied.

3.3 *S. polaris*

The full model included the explanatory variables heat treatment, moisture treatment and week, and the second order interactions between week and heat and moisture treatment (table 3) was selected as the best model.

Table 3 The interacting effect between week and heat and moisture treatment on the number of live shoots of *S. polaris*.

| Random effects: | | | | |
|---|------------------|-----------------|-----------------|----------|
| Groups | Name | Variance | Std.Dev. | |
| Pot ID | Intercept | 0.03 | 0.17 | |
| Number of obs.: 257, groups: pot ID, 29 | | | | |
| Fixed effects: | | | | |
| | Estimate | SE | z | P |
| Intercept | 0.07 | 0.06 | 1.2 | 0.23 |
| Treatment (H3 vs. C) | 0.002 | 0.06 | 0.03 | 0.98 |
| Treatment (H6 vs. C) | -0.04 | 0.08 | -0.49 | 0.63 |
| Treatment (W vs. C) | -0.08 | 0.05 | -1.8 | 0.08 |

| | | | | |
|---------------------------------------|-------|------|-------|--------|
| Week 30 | -0.01 | 0.04 | -0.18 | 0.86 |
| Week 31 | -0.09 | 0.04 | -2.0 | 0.04 |
| Week 32 | -0.26 | 0.04 | -5.9 | <0.001 |
| Week 33 | -0.53 | 0.05 | -11 | <0.001 |
| Week 34 | -1.0 | 0.06 | -19 | <0.001 |
| Week 35 | -1.6 | 0.07 | -23 | <0.001 |
| Week 36 | -4.1 | 0.34 | -12 | <0.001 |
| Week 37 | -3.0 | 0.25 | -12 | <0.001 |
| Week 38 | -6.0 | 0.76 | -7.8 | <0.001 |
| Treatment (H3 vs. C) x Week 30 | -0.03 | 0.05 | -0.50 | 0.62 |
| Treatment (H6 vs. C) x Week 30 | -0.01 | 0.06 | -0.24 | 0.81 |
| Treatment (H3 vs. C) x Week 31 | -0.03 | 0.05 | -0.67 | 0.50 |
| Treatment (H6 vs. C) x Week 31 | 0.002 | 0.05 | 0.03 | 0.98 |
| Treatment (H3 vs. C) x Week 32 | -0.02 | 0.05 | -0.29 | 0.77 |
| Treatment (H6 vs. C) x Week 32 | -0.03 | 0.06 | -0.50 | 0.61 |
| Treatment (H3 vs. C) x Week 33 | 0.05 | 0.06 | 0.93 | 0.35 |
| Treatment (H6 vs. C) x Week 33 | 0.13 | 0.06 | 2.2 | 0.02 |
| Treatment (H3 vs. C) x Week 34 | 0.22 | 0.07 | 3.3 | 0.001 |
| Treatment (H6 vs. C) x Week 34 | 0.33 | 0.07 | 4.8 | <0.001 |
| Treatment (H3 vs. C) x Week 35 | 0.33 | 0.08 | 4.0 | <0.001 |
| Treatment (H6 vs. C) x Week 35 | 0.69 | 0.08 | 8.4 | <0.001 |
| Treatment (H3 vs. C) x Week 36 | 1.2 | 0.36 | 3.5 | 0.001 |
| Treatment (H6 vs. C) x Week 36 | 2.5 | 0.35 | 7.3 | <0.001 |
| Treatment (H3 vs. C) x Week 37 | -0.53 | 0.29 | -1.8 | 0.07 |
| Treatment (H6 vs. C) x Week 37 | 0.63 | 0.26 | 2.4 | 0.02 |
| Treatment (H3 vs. C) x Week 38 | 1.4 | 0.96 | 1.5 | 0.15 |
| Treatment (H6 vs. C) x Week 38 | 0.90 | 0.64 | 1.4 | 0.16 |
| Treatment (W vs. C) x Week 30 | 0.11 | 0.04 | 2.7 | 0.01 |
| Treatment (W vs. C) x Week 31 | 0.08 | 0.04 | 1.8 | 0.08 |
| Treatment (W vs. C) x Week 32 | 0.12 | 0.05 | 2.6 | 0.01 |
| Treatment (W vs. C) x Week 33 | 0.12 | 0.05 | 2.4 | 0.01 |
| Treatment (W vs. C) x Week 34 | 0.11 | 0.05 | 2.0 | 0.05 |
| Treatment (W vs. C) x Week 35 | -0.06 | 0.07 | -0.89 | 0.38 |
| Treatment (W vs. C) x Week 36 | -0.37 | 0.15 | -2.5 | 0.01 |
| Treatment (W vs. C) x Week 37 | -0.38 | 0.19 | -2.1 | 0.04 |
| Treatment (W vs. C) x Week 38 | 1.8 | 0.58 | 3.1 | 0.002 |

Heating does not seem to have an immediate positive effect on *S. polaris*, but it does slow down the rate of senescence towards the end of the heating period (fig.7). From mid-August the controls have the lowest and the 6 heaters have the highest predicted number of green leaves. The effect of the heating can be seen for a couple of weeks after the heating period ended for both water treatments. Heating has a significant effect on *S. polaris*. There is a small but significant interaction during the final weeks of heating and for a few days after for the 6 heater in the dry treatment (table 3, fig. 7).

The wet treatment has generally slightly more predicted green leaves compared to the dry treatment during the heating period (fig. 7). However, post heating in the dry treatment the 6 heater has slightly more green leaves and the senescence is slower compared to that of the 6 heater in the wet treatment. The heating slowed down the senescence from the second half of August, and when the heating ended there were significantly more green leaves in the 6 heaters compared to the 3 heaters and the controls for 1-2 weeks after heating was commenced in both moisture treatments.

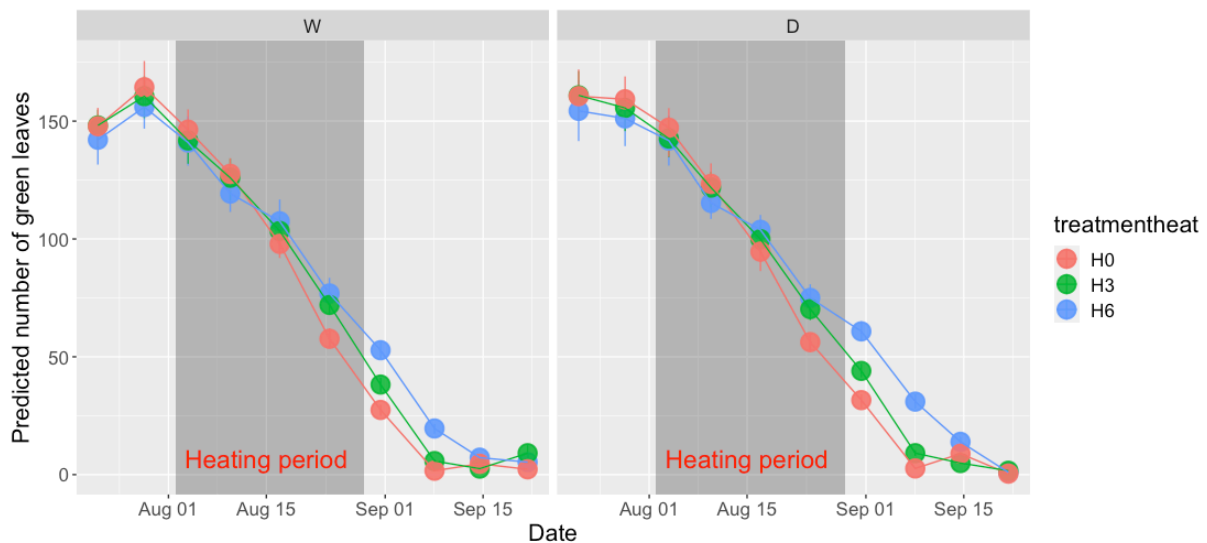


Figure 7 Effects of early heating on *S. polaris*. The left figure shows the change in predicted number of green leaves for the pots that received the wet treatment and the figure to the right show the change in predicted number of green leaves for the pots that received the dry treatment. The red lines show the change in predicted number of green leaves for the pots that had 0 heaters during the study period, the green lines show the same for the pots that had 3 heaters, and the blue lines for the pots that had 6 heaters. The shaded area shows the period for when the heating was applied.

3.4 *B. vivipara*

The final model included the explanatory variables heat treatment and week and their interaction, while the effect of moisture treatment fell out of the model (table 4).

Table 4 The interacting effect between week and heat treatment on the number of live shoots of B. vivipara. There were limited data for some combination of weeks and treatments resulting in some interaction terms involving weeks later than week 35 not being fitted.

| Random effects: | | | | |
|--|------------------|-----------------|-----------------|----------|
| Groups | Name | Variance | Std.Dev. | |
| Pot ID | Intercept | 0.06 | 0.25 | |
| Number of obs.: 191, groups: pot ID, 29 | | | | |
| Fixed effects: | | | | |
| | Estimate | SE | z | P |
| Intercept | 0.02 | 0.11 | 0.17 | 0.87 |
| Treatment (H3 vs. C) | 0.11 | 0.16 | 0.65 | 0.51 |
| Treatment (H6 vs. C) | -0.01 | 0.16 | -0.04 | 0.97 |
| Week 30 | 0.08 | 0.11 | 0.67 | 0.50 |
| Week 31 | -0.19 | 0.12 | -1.6 | 0.10 |
| Week 32 | -0.51 | 0.13 | -4.0 | <0.001 |
| Week 33 | -0.87 | 0.14 | -6.0 | <0.001 |
| Week 34 | -2.0 | 0.29 | -7.1 | <0.001 |
| Week 35 | -3.7 | 1.0 | -3.6 | <0.001 |
| Week 36 | -3.2 | 1.0 | -3.2 | 0.001 |
| Week 37 | -2.4 | 1.0 | -2.3 | 0.02 |
| Week 38 | -2.5 | 1.0 | -2.5 | 0.01 |
| Treatment (H3 vs. C) x Week 30 | -0.15 | 0.17 | -0.86 | 0.39 |
| Treatment (H6 vs. C) x Week 30 | -0.06 | 0.16 | -0.36 | 0.72 |
| Treatment (H3 vs. C) x Week 31 | -0.05 | 0.18 | -0.26 | 0.80 |
| Treatment (H6 vs. C) x Week 31 | -0.01 | 0.17 | -0.04 | 0.97 |
| Treatment (H3 vs. C) x Week 32 | 0.24 | 0.19 | 1.2 | 0.22 |
| Treatment (H6 vs. C) x Week 32 | 0.13 | 0.18 | 0.72 | 0.47 |
| Treatment (H3 vs. C) x Week 33 | 0.38 | 0.21 | 1.8 | 0.08 |
| Treatment (H6 vs. C) x Week 33 | 0.39 | 0.19 | 2.0 | 0.05 |
| Treatment (H3 vs. C) x Week 34 | 1.0 | 0.35 | 2.9 | 0.004 |
| Treatment (H6 vs. C) x Week 34 | 0.90 | 0.33 | 2.7 | 0.01 |
| Treatment (H3 vs. C) x Week 35 | 2.8 | 1.1 | 2.7 | 0.01 |
| Treatment (H6 vs. C) x Week 35 | 2.2 | 1.0 | 2.1 | 0.03 |

| | | | | |
|--------------------------------|------|-----|------|------|
| Treatment (H3 vs. C) x Week 38 | 0.03 | 1.2 | 0.03 | 0.98 |
|--------------------------------|------|-----|------|------|

Heating has a positive effect on *B. vivipara*, and there is a significant interaction between week and the heat treatments that can be seen during and shortly after the heating period (fig. 8). Both heat treatments have a higher predicted number of green leaves compared to the control during the heating period. However, the 3 heater has a higher predicted number than the 6 heater, which was not expected. The heating slowed down the senescence during the heating period and the following two weeks. When the heating ended there were few green leaves left, but there were notably more green leaves in both heat treatments compared to the control for 1-2 weeks after heating was commenced.

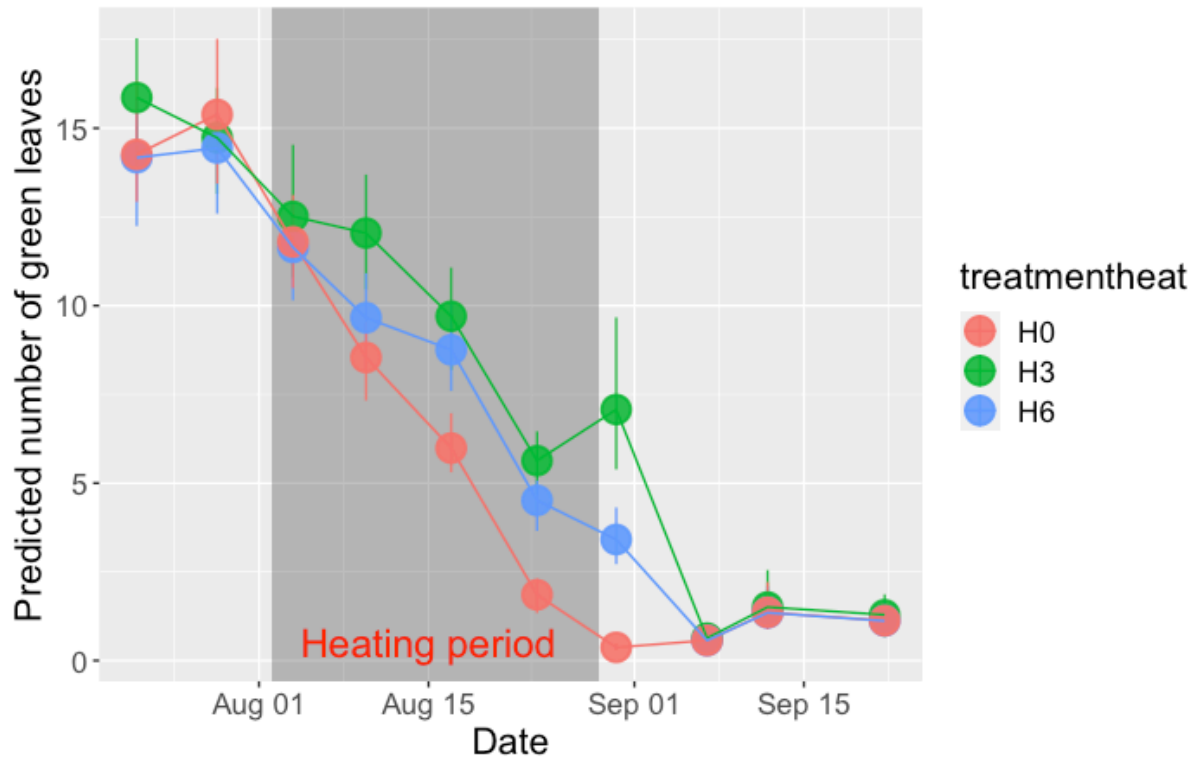


Figure 8 Effects of early heating on *B. vivipara*. The red line shows the change in predicted number of green leaves for the pots that had 0 heaters over the study period, the green line shows the same for the pots that had 3 heaters, and the blue line for the pots that had 6 heaters. The shaded area shows the period for when the heating was applied.

4. Discussion

There is a lack of studies concerning how climate change will affect plants during the end of the growth season. In this study, I have examined the effect raised temperatures and moisture levels in summer will have on the onset and rate of senescence on three of the most common

foraging plants of the Svalbard reindeer. I found that all three of the study species responded positively to heating. *S. polaris* responded positively to an increase in moisture, while it had no effect on the other two. Onset of senescence was delayed for *A. ovatus* and partly for *B. vivipara*, while the rate of senescence was slowed for *B. vivipara* and *S. polaris*. Based on my results *A. ovatus* will benefit the most from a warmer climate, while *B. vivipara* will benefit the least, and particularly in a climate resembling that of the 6 heater in this study as it may be limited by a lack of soil moisture. A warmer climate during the snow-free period with a prolonged end of growth season seems to counteract the negative effects of harsh, icy winters on the Svalbard reindeer. The increase in biomass may positively affect the body mass and survival rate of the Svalbard reindeer, and hence lead to population growth.

4.1 Effects of increased temperature and soil moisture levels on the study species

All three species had a positive response to increased temperatures. Onset of senescence in green biomass for *A. ovatus* was delayed with approximately 3 and 4 weeks for the 3 heater and 6 heater, respectively. However, there was no clear pattern for a slower rate of senescence after heating commenced. The positive response in green biomass came from increased length and not count as the count of green leaves showed no response to the heat treatments. *S. polaris*, on the other hand, showed no clear pattern for a delay in onset of senescence, but had a slowed rate of senescence. *B. vivipara*'s 3 heater had a delay in the onset of senescence with approximately one week, but there is no clear pattern for a delay for the 6 heater. Moreover, the rate of senescence was also slowed for both treatments during the heating period and for the following two weeks after the heating commenced for *B. vivipara*.

S. polaris was the only species that showed a positive response to moisture while the two other species stayed neutral to this treatment. The 6 heater had the highest number of predicted green leaves independently of the moisture treatments, suggesting that heat is more important than moisture for *S. polaris*. Yet, early senescence has been found in systems that are water-limited (Livensperger et al., 2019; Westergaard-Nielsen et al., 2017), and Winkler et al. (2016) found that a warmer climate in alpine systems were largely contingent upon available soil moisture and that both shrubs and forbs would have a larger increase in a climate that was both warmer and wetter, suggesting that *B. vivipara* and *S. polaris* could be limited by moisture in a future climate scenario that is both warmer and drier. However, the climate is expected to become warmer and wetter the next 80 years (Adakudlu et al., 2019),

and water limitation is not expected to significantly affect these species. Additionally, my fellow master student Andersen (2023), who investigated the effects of increased soil moisture on the same three study species, found that they all responded positively to moderately increased soil moisture levels and that *B. vivipara* and *S. Polaris* could struggle under high soil moisture levels as they were more sensitive to oxygen deprivation due to their shallow root systems. This implies that the lack of response to moisture found in my results could be a result of a too low increase of the moisture level as the species received substantially more water in Andersen's (2023) experiment. Additionally, my experimental levels for moisture were also comparably lower than my experimental levels of heat applied and may further explain the lack of response to increased soil moisture.

My results aligned for the most part with the results of former master student Kinyua (2022). She found that elevated autumn temperatures, but not moisture, positively affected *A. ovatus* and *B. vivipara*, but not *S. polaris*. By manipulating the summer temperatures instead, I found that both temperature and moisture positively affected *S. Polaris* as well. The difference in response to temperature may be a result of an early onset of senescence for the species in combination with an implementation of autumn heat that was too late to have any effect on it. Further, water-limitation for *S. polaris* and *B. vivipara* may also have affected the results of Kinyua (2022), and research combining increased temperatures with moisture levels similar to those of Andersen's (2023) could be beneficial to better understand the climate induced changes to the plants in Svalbard.

4.2 Expected changes in future vegetation composition and implications for the Svalbard reindeer

Increased summer temperatures resulted in a delay of onset of senescence and slowed rates of senescence for all three study species. *S. Polaris*, and possibly also *B. vivipara* (Andersen, 2023), seem to be more limited by soil moisture levels than *A. ovatus*, but with a predictably warmer and wetter climate (Adakudlu et al., 2019) these changes in senescence should lead to an increase in plant biomass as well as an extended growth season in autumn. This should allow for a longer period with higher quality forage for the Svalbard reindeer to build up their fat reserves before the winter and hence improve their winter survival rate (Albon et al., 2017; Loe et al., 2021; Tews et al., 2007).

A few studies have argued for a greening of the Arctic, possibly through shrub encroachment, in the High Arctic (Hudson & Henry, 2009; Myers-Smith et al., 2015). However, Kapfer et al. (2017) could not find support for a “shrubification” of the High Arctic. They found indications of a starting phase of a greening process, but with an increased frequency of several grass species, such as *A. ovatus*, and the dwarf-shrub *S. polaris*. My results indicate that *A. ovatus* may benefit the most out of my three study species from increased temperature and moisture levels in the summer, supporting the findings of Kapfer et al. (2017). However, Kapfer et al. (2017) argued that the increased occurrence of *A. ovatus* could be a result of increased grazing by herbivores (Kapfer et al., 2017) as grazing facilitates growth through the positive feedback loop between the herbivore and its preferred foraging plants (Van der Wal & Brooker, 2004). Hence, we might see an even larger increase in plant biomass and distribution of *A. ovatus* and other preferred grass species by the Svalbard reindeer in the future due to grazing.

In addition, trampling and fertilization through feces by the Svalbard reindeer may also promote more biomass for at least grass species. The trampling reduces the depth of the moss layer, which is negatively impacting moss species, but allow for increased soil temperatures and better growth conditions for the grass species. Arguably, it may also increase the availability of nitrogen in the soil which could be beneficial for vascular plants, and particular for grass species (Van der Wal & Brooker, 2004). However, Van der Wal & Brooker (2004) specify that their results only showed growth in response to trampled moss when the moss layer was initially relatively deep and that the grass cover dropped again if the moss layer became too thin. These interactions with the Svalbard reindeer would promote further growth of *A. ovatus* in addition to those caused by increased temperatures in response to climate change. Additionally, fertilization through feces and urine will add additional nutrients for *S. Polaris* and *B. vivipara*, as well as for *A. ovatus* (Van der Wal & Brooker, 2004). The effects the Svalbard reindeer may have on their feeding plants could be expected to increase with the potential population growth that could occur in response to the increased level of higher quality forage over a prolonged autumn season, hence enforcing a positive feedback loop.

High quality forage is normally preferred over high quantity forage by herbivores as the consumption of low-quality forage leads to low nutrient intake and hence low digestibility due to high lignin and fiber content (Prop & Vulink, 1992; Robbins, 1993; Van Soest, 1994), resulting in a reduced total intake of digestible matter (Van der Wal et al., 2000). However,

Van der Wal et al. (2000) found that the Svalbard reindeer selected the advanced spring plots due to greater biomass, despite that these plots had the lowest plant quality, suggesting that the Svalbard reindeer selected based on quantity over quality. Despite these findings contrasting with the herbivores in temperate regions, they argue that it might be an outcome of the generally low levels of both biomass and high quality forage during the growing season in Svalbard. The increase in biomass, which my results suggest, could hence be positive for the Svalbard reindeer and to some extent independent of the quality of the biomass.

Due to the absence of predators, the Svalbard reindeer are most likely regulated by their interaction with food, also known as “bottom-up” controlled (Loe et al., 2021). Delayed autumns seem to enhance the nutritional landscape for the herbivores (Hurley et al., 2014; Parker et al., 2009), and have been associated with higher body mass in the Svalbard reindeer (Albon et al., 2017). Body mass is a convenient measure of body condition of the Svalbard reindeer (Parker et al., 2009) as it continuously responds to weather and the population density, which is affected by the food availability and energy expenditure (Bårdsen & Tveraa, 2012). Hence, body mass is a suitable variable in finding the effects of seasonally varying environmental drivers on the Svalbard reindeer (Taillon et al., 2011). Higher body mass in the Svalbard reindeer, as a result of increased availability of foraging plants, should enhance body growth, fecundity and survival (Parker et al., 2009), and consequently lead to population growth (Loe et al., 2021). However, mortality rates are strongly related to winter condition (Albon et al., 2017) and the occurrence of extreme ROS events (Putkonen & Roe, 2003; Rennert et al., 2009) as they depress late winter body mass and can lead to starvation due to ice-locked pastures (Gunn, 2020; Hansen et al., 2011; Kohler & Aanes, 2004), and result in reduced population growth rates (Hansen et al., 2013; Hansen et al., 2019). However, both Loe et al. (2021) and Albon et al. (2017) found that prolonged autumns counteracted these negative effects of harsher, icy winters, and promoted higher population densities for the Svalbard reindeer. If the results of Loe et al. (2021), Albon et al. (2017) and myself prove to be correct, it suggests that the net effect of a warmer climate on both the foraging plants of the Svalbard reindeer and the reindeers themselves will be positive and that the future of the Svalbard reindeer may be brighter than previously thought (Mallory & Boyce, 2018; Vors & Boyce, 2009).

5. Conclusion

My results suggest that a warmer climate will benefit all three study species. However, *S. polaris* and *B. vivipara* might experience water-limitations if the soil is not sufficiently wet in the future. Onset of senescence was delayed for *A. ovatus* and *B. vivipara*, lengthening the end of the growth season. Additionally, rate of senescence was slowed for *S. polaris* and *B. vivipara*, providing more biomass during summer and autumn. The delay in onset and slowed rates of senescence for all the species found in this thesis should all positively affect the Svalbard reindeer as they prolong the unrestricted foraging period. A warmer climate with such positive effects will most likely counteract the negative effects caused by harsh winters on the Svalbard reindeer, and hence lead to further population growth.

To heighten the understanding of climate induced changes to the terrestrial system of Svalbard it is advised to include the change in biomass for *S. polaris* and *B. vivipara*, study the effects of fertilization by the Svalbard reindeer, and study other promoters and inhibitors of the different foraging plants such as soil nitrogen availability.

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Appendix

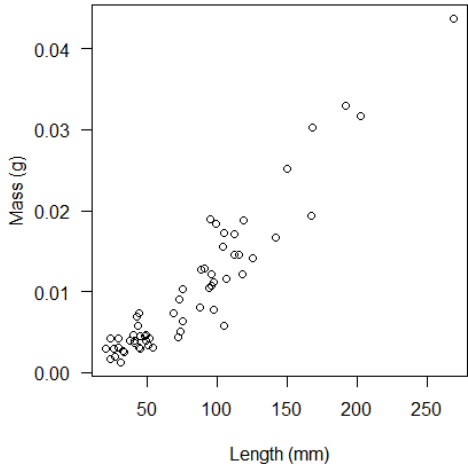


Figure 9 Shows the distribution of *A. ovatus* individuals' lengths (x-axis) and weights (y-axis) measured to obtain biomass.



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