



Norwegian University
of Life Sciences

Master's Thesis 2022 60 ECTS

Faculty of Environmental Science and Nature Management

Effect of autumn warming on the rate of senescence in Svalbard plants: An experimental approach with relevance for Svalbard reindeer

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MSc. Ecology

Dedication

This Master's Thesis is dedicated to my husband (Joel Otieno Odhiambo), my son (Juan-Willian Agunda Otieno) and my late mother (Jane Wambere Mwangi).

Acknowledgements

This Master's thesis is submitted as a final and integral part of the Master of Science in Ecology at the Norwegian University of Life Sciences (NMBU) in Ås, Norway. It was conducted as part of the Reindeer Project in Svalbard "Svalbardrein" under the supervision of Professor Leif Egil, Professor René Van Der Wal, and Samantha Paige Dwinell.

First, I would like to thank God for making it thus far. The completion of this thesis would not have been possible without the expert guidance of Professor Leif Egil. He has been immensely supportive from the beginning to the last moments of shaping this thesis document. I have learned, experienced, and I hope to share these lessons with the world. I want to thank him and the Svalbardrein project for allowing me the opportunity of a lifetime to go to Svalbard and join this project. It was eye-opening and substantially educative, and I am forever grateful to him. I would like to thank Professor René Van Der Wal for his contribution towards setting up the experiment and teaching me the technicalities of a manipulative experiment. I would like to thank Sam, who was with me from the beginning to the end of setting up the project and data collection at the old Northern Lights Station. Her guidance, encouragement, teaching and making the work easier and fun. I would like to thank the whole team at the NTNU cabin, especially Emma, who was with me for the largest part of the data collection. We braced the cold, windy days together, and we enjoyed the limited, calm sunny days with smiles. I would like to thank Svalbard for this experience. Longyearbyen is a town etched in my heart. UNIS is a futuristic university with a community of knowledgeable individuals who constantly shared information to help others.

I would like to give special thanks to my family and friends. My husband and my parents-in-law for their support during this time. My son for being such a brilliant gentleman who is already taking the world by a stride. I am a proud mother. I would like to thank my sister and her family for always being there for me. My grandparents have always been an integral part of my life and encouraged me to pursue my dreams.

Norwegian University of Life Sciences

May 2022

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Abstract

Phenology is a biological trait sensitive to global warming. Climate change scenarios predict a three-fold increase in temperature and altered rainfall for polar regions. The Svalbard Archipelago, situated at 78° North, and 15° East, is a hotspot for climate change in the arctic, and my study was in the Adventdalen valley of the island. According to climate models, the average annual temperature will increase by about 10°C, while the autumn temperature will increase between 7-10°C by 2100. My study was an experiment manipulating temperature (open top chambers in combination with heaters elevating temperature by ca. 2 and 7 degrees) and moisture (dry and wet) to investigate their impact on rate of senescence in autumn in three Svalbard reindeer (*Rangifer tarandus platyrinchus*) forage species. The three species also constitute the three dominant growth forms in Svalbard. *Alopecurus borealis* represented graminoids, *Bistorta vivipara* represented forbs, and *Salix polaris* represented shrubs. It was a transplant experiment to a garden with 12 plots. Counts of green and brown shoots/ leaves were done for about six weeks in late summer-autumn, beginning in mid-August to the end of September when freezing occurred. I found that the graminoid delayed the rate of senescence with higher temperature and moisture. The forb was not affected by moisture but showed a moderate delay in rate of senescence with higher temperatures, while neither moisture nor temperature affected the autumn phenology of the shrub. My analysis shows contradictory results to various other studies that have suggested a greening arctic due to shrubification in the arctic tundra. Graminoids may be the winners of climate change effects in autumn and may affect herbivores positively, by increasing their autumn food quality. Therefore, warmer, and wetter autumns may counteract the effects of harsh winters and propagate the reproductive success of the Svalbard reindeer. As capital breeders, Svalbard reindeer may access higher quality and quantity of vegetation late into autumn and pack fat reserves for over-wintering. My study is just the beginning of a journey toward understanding the link between food availability in autumn and the enhanced fitness of the Svalbard reindeer.

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1 Introduction

Phenology, the timing of biological life-cycle events in organisms, is one of the most sensitive biological traits to a changing climate (Fitchett et al., 2015). One study suggests that climate change explains 66% of the year-to-year changes in phenology (van Vliet et al., 2014). Plant phenology responds specifically to local climate change, such as warmer temperatures and altered rainfall (Fitchett et al., 2015). Although numerous studies have focused on winter, summer and spring phenology, few studies have focused on autumn phenology. The goal is to establish a wholesome understanding of plant phenology, caused by a changing climate, with the arctic as my area of interest.

Hanssen-Bauer (2019) estimated that the poles are experiencing two or three times more pronounced warming than the mean for the rest of the world. In the Arctic Archipelago of Svalbard, the temperature predictions imply an increase of 10⁰C for high emissions and about 7⁰ C for medium emissions by 2100 (Hanssen-Bauer et al., 2019). At the same time, predictions for autumn temperature increase lie between 7.4 – 10.3⁰C (RCM ensemble) and 7.1 –10.0⁰C (ESD ensemble) by 2100. For precipitation, the prediction is more frequent rainfall annually, and between 40-56 % increase in autumn rain. In combination, this predicts a shortening of the snow season in the latter 21st Century. Hanssen-Bauer et al., (2019; McCrystall et al., 2021); report that the climate in the arctic in the 21st Century will impact the water cycle. It will result from higher evaporation after sea ice loss, leading to more open water and corresponding climate feedbacks. The atmosphere in the arctic will carry more moisture, and a shift from a snow-dominated system to a rainfall-dominated system will occur (McCrystall et al., 2021). Moisture, therefore, is as important a factor for climate change in the arctic ecosystem as temperature.

The Arctic is highly responsive to this changing climate due to its low productivity and a bottom-up regulated ecosystem (van der Wal & Stien, 2014). The arctic plants, being significantly temperature limited (van der Wal & Stien, 2014) may show pronounced changes in their phenology (Collins et al., 2021; van der Wal & Stien, 2014). For instance, Svalbard is snow-covered for eight months of the year. It limits the growth of vascular plants to a short and variable growing season. The ground is often snow free from early to mid-June, biomass peaks in July/August before senescence kicks in, and plants are dead by September/October (van der Wal & Stien, 2014). Several Svalbard habitats consist mainly of bryophytes such as mosses with sparsely growing vascular plants that do not attain much height (van der Wal & Stien, 2014). The higher temperature and rainfall occurring in the arctic raise the question of

the substantial changes in the annual plant phenology responses arising from these novel and unprecedented events. Moreso, the interactive effects between temperature and rainfall (Jespersen et al., 2022) as the leading factors in the phenological responses, and the plants' responses thereto.

Climate-change effects on plant phenology will undoubtedly influence herbivores (Gustine et al., 2017). In an unstable environment, consumers will adapt to match the costliest life-history events, typically reproduction, with the season's highest resource availability (Doiron et al., 2015). The growing season provides the highest resource for herbivores and its length relies on the onset of snowmelt in spring and the onset of dormancy in autumn. Ernakovich (2014; van Vliet et al., 2014) found evidence of a longer growing season due to warming and due to moisture (Li et al., 2020) in the Tibetan plateau. Some studies have also claimed that climate warming promotes shrub expansion in the tundra (Black et al.; Parker et al., 2021), leading to a greener arctic. Global warming is causing an earlier onset of plant growth and, therefore, higher plant productivity, increasing food available for arctic herbivores (Tveraa et al., 2013). There have been some concerns that altered spring phenology will cause a trophic mismatch effect, consequently depressing the reproductive success of herbivores (Doiron et al., 2015), although this has been disputed (Gustine et al.; Veiberg et al., 2017). Research shows that climate change effects on summer and autumn biomass match the requirements for caribou and their young ones to accumulate mass for the following year's reproduction and over-wintering (Gustine et al., 2017). That means that the most crucial season for northern ungulates occurs in late summer-autumn because minimal changes in forage quality and quantity have compounding effects on mass gains and reproductive success of northern ungulates (Gustine et al., 2017). Therefore, the population growth or decline of herbivores is highly dependent on the nature of the growing season. The nuances above support the admission by many studies that arctic herbivores are facing the world's fastest changes in the amount and timing of their food supply (Flint & Meixell; Loe et al., 2021). The concern lies heavily on how climate warming will influence the plants used as forage by herbivores and the timing of their phenology, and how this will, in turn, affect the herbivores that rely on them (Chisholm et al., 2020). Studies have shown links between autumn and winter conditions and the body mass of *Rangifer tarandus platyrhynchus* populations (Albon et al., 2017). However, investigations into the biomass and quality of forage species in these ecosystems during autumn are lacking.

A suggestion is that autumn phenology is majorly affected by temperature. A study by (Li et al., 2020) found that temperature effectively delayed the autumn phenology in a

Tibetan plateau, with correlations as high as 71% in the study areas. Senescence may begin early if the temperatures are low (Zhang et al., 2020). A study by (Zhu et al., 2017) showed highly variable autumn phenology that implied that climate change impacts plant species, temperature, and even phenological events. Studies of autumn phenology are more challenging than the other seasons because autumn phenology is not as definitive as spring. Phenological events in autumn occur over a relatively long period and thus pose challenges to observational processes. An autumn phenological event depends on the observer to decide the degree to which phenology has occurred (Gallinat et al., 2015). More investigation is required to enhance accurate predictions of future climate change impacts on plant phenology and ecosystem responses to global warming during autumn.

In my master thesis, I have designed a manipulative experiment to investigate the effects of temperature and moisture on the rate of senescence in the arctic. My study uses the three major Svalbard reindeer forage species as representatives of different growth forms in the arctic namely, graminoids, forbs and shrubs. The experiment has explored the underlying mechanism that drives the rate of senescence of these plant species and how this varies between diverse levels of treatment anticipated with future climate change as stipulated in climate models. My hypotheses are:

- i. The warming climate in autumn will delay the rate of senescence in Svalbard reindeer forage species.
- ii. Higher precipitation expected in the arctic in autumn will delay the rate of senescence in Svalbard reindeer forage species.

2 Materials and methods

2.1 Study area

Svalbard lies at 78° North, and 15° East. My experimental site was in the valley of Adventdalen in Svalbard, Norway. The average annual temperature for the period 1981-2010 (Svalbard Airport) was -4.6°C, with -3.5°C in autumn and much lower, -11.7°C, for the winter months (Forland et al., 2011). The average annual precipitation for the same period was 191mm with 58mm for autumn months. Vegetation is scarce, short without trees, and highly affected by fluctuating climate (van der Wal & Stien, 2014). Permafrost keeps a high-water table making the valleys of predominantly wet vegetation types.

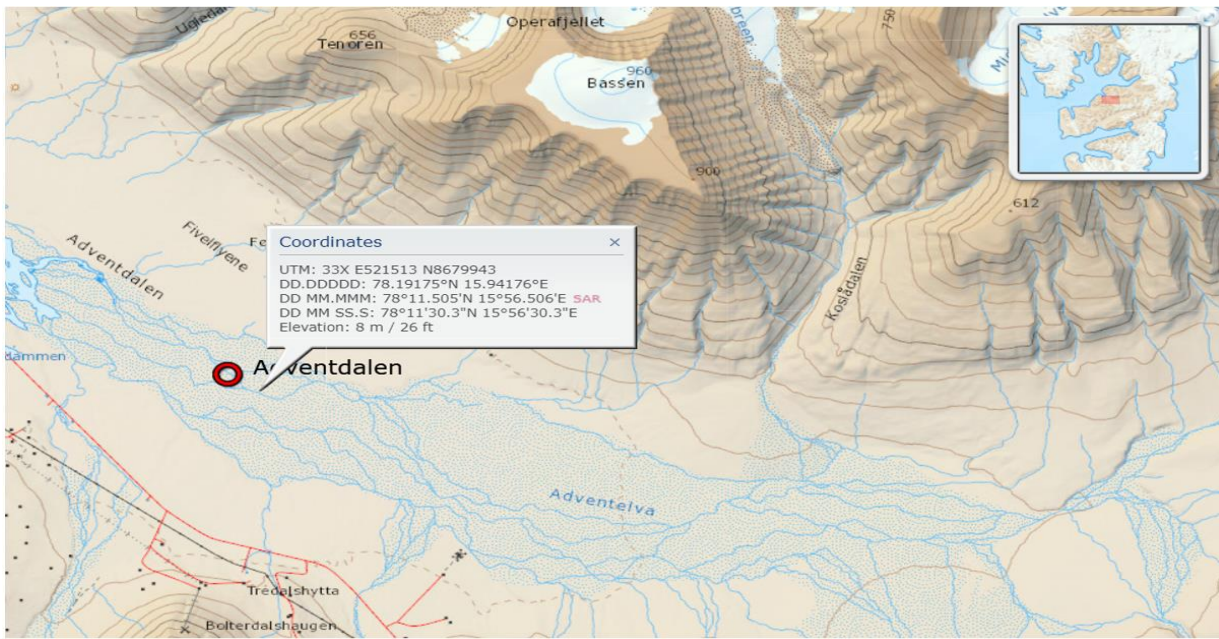


Figure 1. An image of the study area, Valley of Adventdalen in the Svalbard Archipelago. Source: <https://toposvalbard.npolar.no/>

2.2 Study Species and design

My study focus was on the main reindeer forage species from three major growth forms of arctic plant species. These are among the species that they use most during the growing season.

The species of focus include:

1. Graminoids
 - a. *Alopecurus borealis* (boreal Alopecurus)
2. Shrubs
 - a. *Salix polaris* (polar willow)
3. Forbs
 - a. *Bistorta vivipara* (alpine bistort)

The aim of my study was to establish the effect of heating and moisture treatments on *Bistorta vivipara*, *Alopecurus borealis*, and *Salix polaris*. Pots, measuring 20cm in diameter, were identified in the Adventdalen valley and cut out, marked, and put back into the soil as they awaited transplantation to the garden. This is where the experiment was carried out for the rest of the fieldwork. The pots were subjected to both heat and moisture treatment as the focal point of my investigation.

The garden setup had 12 plots. Each plot represented either of the three heat treatments (0,2,6 heaters) or a control. The heaters used were 200W and the different number of heaters in each plot was to ensure a heating gradient. The treatments were divided into 3 main levels of heating (Fig. 2) mainly, Control (No OTC, no heater), low heat (OTC, no heater), medium heat (OTC, plus 2 heaters), and high heat (OTC, plus 6 heaters).

Within each plot (OTC) were two pots. The pots represent the two-moisture regimes, that is, wet and dry vegetation. The dry treatment was watered with 0.5L of water twice a week, while the wet treated pots were watered with 0.5L of water four times a week. Overall, I had 24 pots; 12 pots of vegetation wet (VW) and 12 pots of vegetation dry (VD).

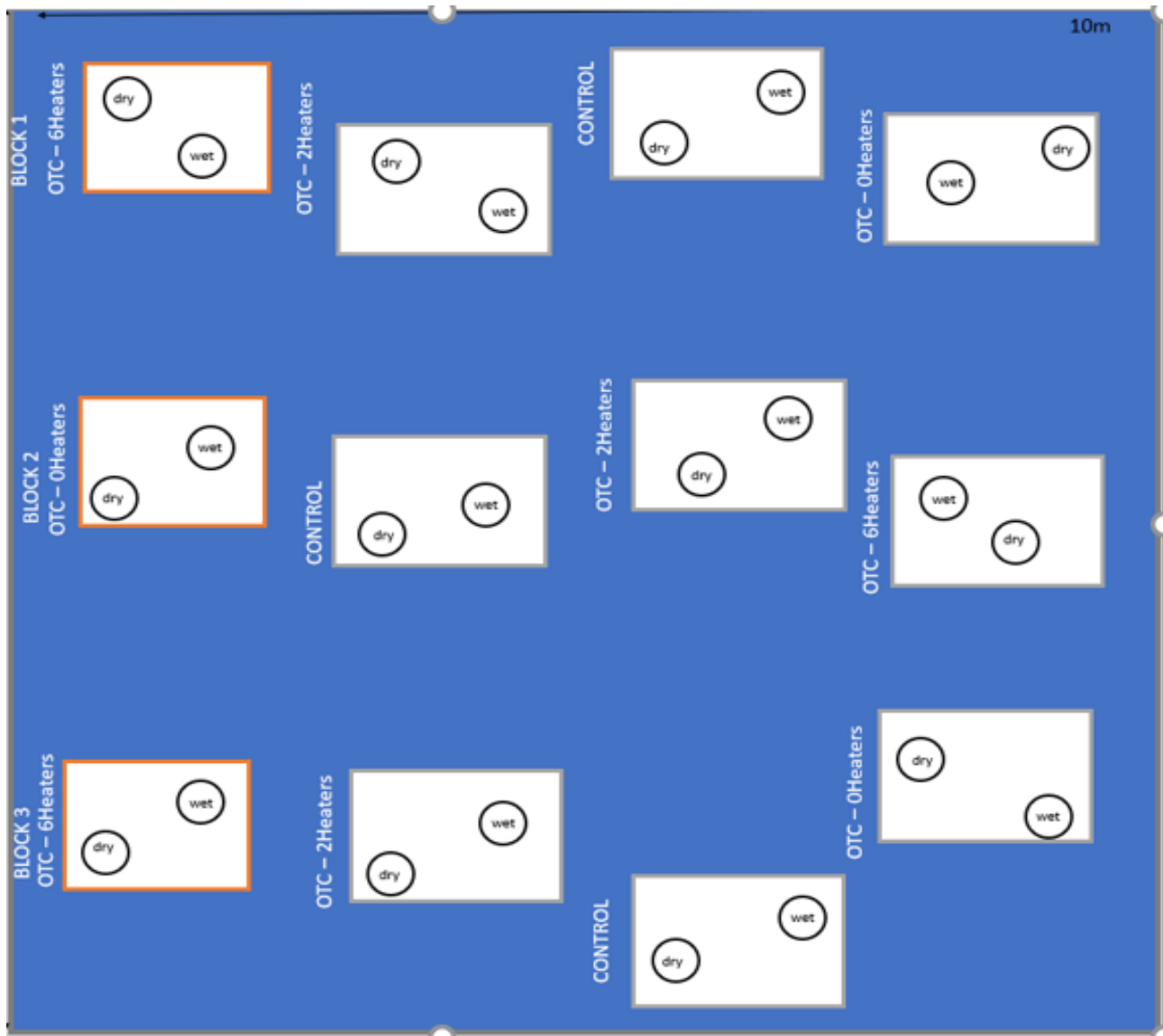


Figure 2: A visual representation of the garden experiment set up, with both dry and wet pots and division into 3 blocks. The image also shows how each arrangement was also set up with control, 0 Heaters (just an OTC added), 2 Heaters, and 6 heaters to give a varying degree of the heat treatment. The pots were set up randomly across the garden.

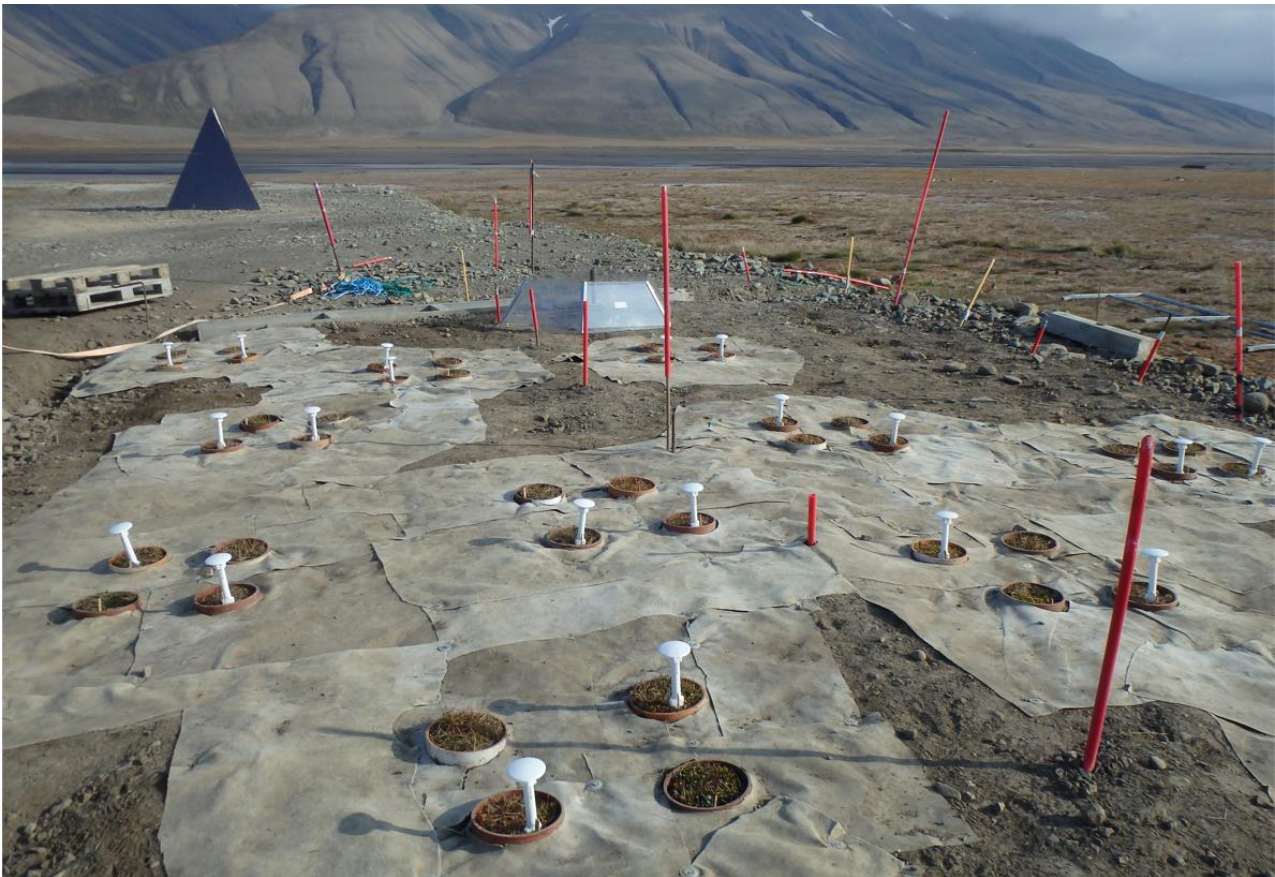


Figure 3: A cross-sectional picture of the garden set up at the Old Northern Lights Station in Adventdalen. The picture shows the data loggers that were used to record temperature in the pots, as well as a visual representation of the 20cm diameter pots.

2.3 Data collection

Senescence measurements were done in the garden during the late summer months up to autumn, the beginning of October when freezing occurred and the garden was covered in snow. Sampling was done once a week.

The first measurement (Week 1) of senescence occurred before heating was put in place. This was 4 days before the installation of the heating treatment. The measurements in the progressive weeks (Week 2 (16th-20th August 2021) – Week 7 (30th September 2021)- for *Alopecurus borealis*) were done after the installation of the heating system.

For *Alopecurus borealis*, I counted both the leaves and the number of plants in one pot. I then recorded the length in millimetres, of the different colours on the leaves as senescence occurred. The colours to show the rate of senescence were green, red, yellow, and brown.

For *Salix polaris*, I counted the number of leaves in a pot with the assumption that it was one plant per pot. I recorded the colour of the leaves depending on what stage of senescence the leaves were at, that is green, red, and yellow.

For *Bistorta vivipara*, I counted the number of plants and then the number of leaves per plant. The rate of senescence was measured as the proportion of green leaves remaining at each stage of the measurements.



Figure 4: A picture of the 20cm diameter pot used in transplantation during the experiment. The image shows the distribution of the three species of interest in the pot, as well as an identification for the pot (VD06).

2.4 TMS Dataloggers

TMS dataloggers, from the company TOMST® from Dallas, from the United States of America. were installed in all the pots to make temperature recordings during the time of the investigation. The dataloggers automated the temperature recordings within the pots. The loggers have three temperature sensors. Temperature sensor 1 recorded soil temperature approximately 5cm below the surface of the ground. Temperature sensor 2 was recorded approximately 2cm above the soil surface, while temperature sensor 3 was recorded approximately 10cm above the surface. The temperature was recorded every 15 minutes during the data collection period. Lolly program was used to download the data recorded and the analysis of the temperature data was done in R.

2.5 Statistical Analysis

Data was analysed using R version 4.2.0 (R Core Team 2021). The models used were generalized linear mixed model fit by maximum likelihood ratio. Pot ID was set as a random factor. Each of the three species were analysed in separate models. The response variables were a measure of greenness for the different species. For *Alopecurus borealis*, I used if the shoot was partly or fully green (yes=1, no=0) as a binomially distributed response variable. For *Salix polaris* and *Bistorta vivipara*, I used the count of green leaves as a response variable (assumed to follow a Poisson distribution). The candidate predictor variables were moisture (two-level factor variable: dry and wet), heat treatments (4-level factor variable: control [No OTC, no heater], low heat [OTC only], medium [OTC + 2 heaters], and high [OTC + 6 heaters]), week (factor variable with one level per week), and all interaction up to the three-way interaction. I used backward model selection using likelihood ratio tests (Pinheiro & Bates, 2000) to identify the best fit models for all the species. The impact of treatment effects on the rate of senescence was supported if two or three-way interactions involving the treatment effects and week were included in the final models.

3 Results

3.1 TMS Dataloggers

Six heaters in an OTC (termed H6) were able to warm up plots by about 6^o- 8^oC (Fig. 3) compared to the control. The two heaters in an OTC (termed H2) increased the temperature by about 2^oC and the OTC-only plot (termed H0) was not different from the control. Towards the end of the experiment, the H6 treatments were still about 10^oC even when temperatures were close to the freezing point in other treatments and the study area.

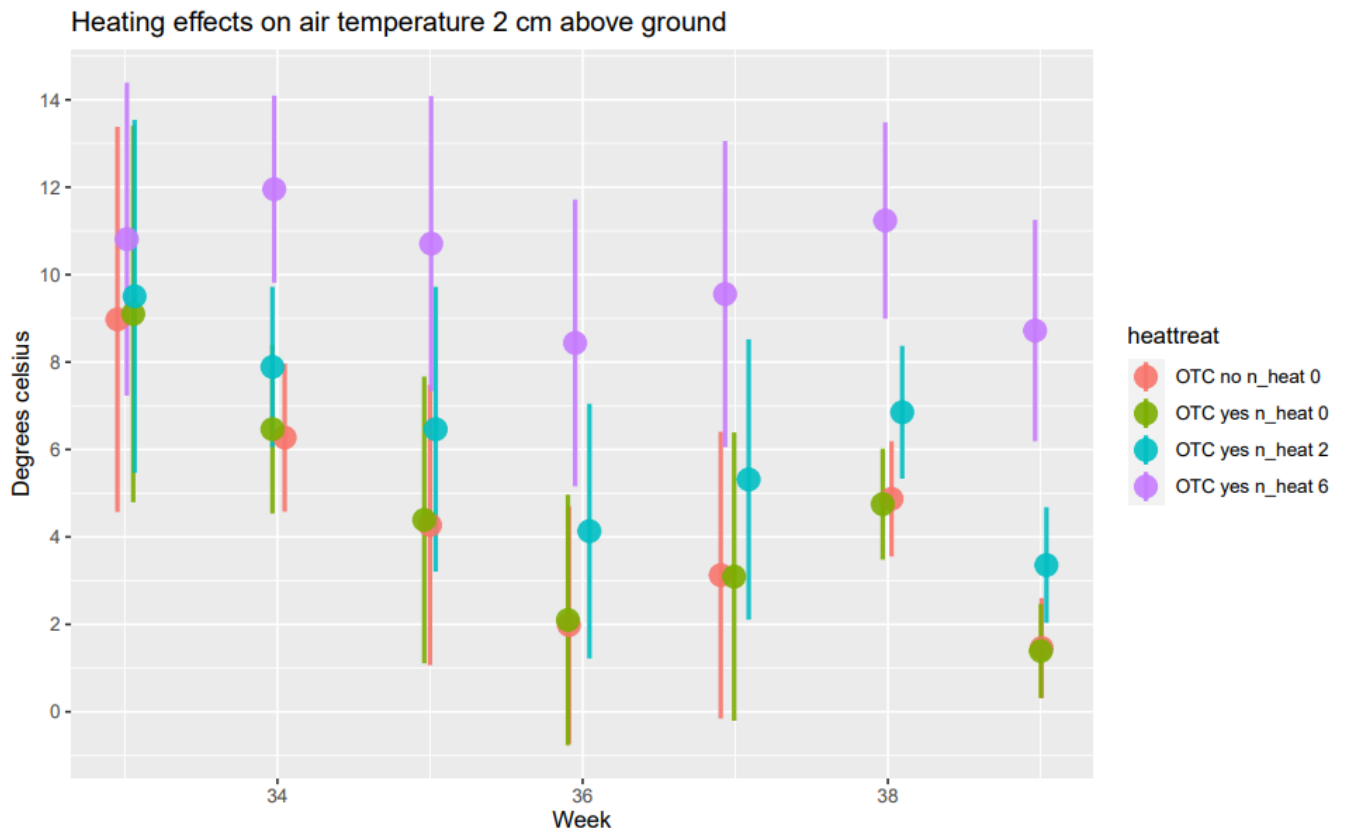


Figure 5: Weekly temperature means for different heating levels. The highest recorded temperature was from treatment plots with 6 heaters which was about 6-7^oC higher than the control. The lowest temperature recorded was from both the control and the low heat(H0). The low heat treatment was not significantly different from the control. 2 heaters provided about 2^oC higher temperature than the control. The error bars represent 95% confidence limits.

3.2 Effects of heating and moisture treatments on rate of plant senescence

3.2.1 *Bistorta vivipara*

The initial number of green *Bistorta* leaves per pot was quite variable even before the heating experiment commenced, resulting in an unplanned difference in the mean number of green leaves per treatment level. The highest number of green leaves, just above 21 green leaves, was in the H6 and the control pots. H2 treatment pots had the lowest number of green leaves (Fig. 6). However, I could still evaluate the treatment effect on the rate of senescence through the interaction between week and the two types of treatment. The final model (model bispo5; Table 1; Table 4 in supplementary) included the interaction between heat treatment and week, while all terms involving moisture treatment fell off during the model selection. The H6 pots had the highest predicted number of green leaves by week three and week four. The predicted number of green leaves dropped rapidly from around 15 green leaves in week 1 (before treatment started) to week 3, when typically, less than five green leaves per pot remained. While there was no pronounced heating effect in weeks 2 and 3, H2 treatments had more green leaves in week 3 as compared to week 2 and the control. The H2 pots approached control plots with around two green leaves in week four, while senescence was delayed in H6 pots (Fig. 6).

Table 1: *A generalized linear mixed model fit by maximum likelihood of the family Poisson for *Bistorta vivipara*. Potid was fit as a random effect. The final model showed a significance for the interaction between heat treatment and week at $p < 0.01$.*

bispo1 <- glmer (leafno ~ treatmentheat*treatmentmoist*week+(1 potid), data=bis.green.count,family=poisson)								
bispo2 <- glmer (leafno ~ treatmentheat + treatmentmoist + week + (1 potid) + treatmentheat: treatmentmoist + treatmentheat: week +treatmentmoist: week, data=bis.green.count, family=poisson)								
Mod.	npar	AIC	BIC	logLik	devianc	Chisq	Df	Pr(>Chisq)
bispo2	24	454.41	510.97	-203.21	406.41			
bispo1	32	466.6	542.01	-201.3	402.6	3.8143	8	0.8735
bispo3 <- glmer (leafno ~ treatmentheat + treatmentmoist + week + (1 potid) + treatmentheat: treatmentmoist + treatmentheat: week, data=bis.green.count, family=poisson)								
bispo3	21	450.43	499.93	-204.22	408.43			
bispo2	24	454.41	510.97	-203.21	406.41	2.0237	3	0.5675
bispo4 <- glmer (leafno ~ treatmentheat + treatmentmoist + week + (1 potid) + treatmentheat: week, data=bis.green.count, family=poisson)								
bispo4	18	449.9	492.33	-206.95	413.9	Chisq	Df	Pr(>Chisq)
bispo3	21	450.43	499.93	-204.22	408.43	5.47	3	0.14044
bispo5 <- glmer (leafno ~ treatmentheat+ week + (1 potid) +treatmentheat: week, data=bis.green count, family=poisson)								
bispo5	17	448.2	488.27	-207.1	414.2			
bispo4	18	449.9	492.33	-206.95	413.9	0.2998	1	0.584
bispo6 <- glmer (leafno ~ treatmentheat+ week + (1 potid)_ data=bis.green.count, family=poisson)								
bispo6	8	452.05	470.91	-218.03	436.05			
bispo5	17	448.2	488.27	-207.1	414.2	21.848	9	0.009375**

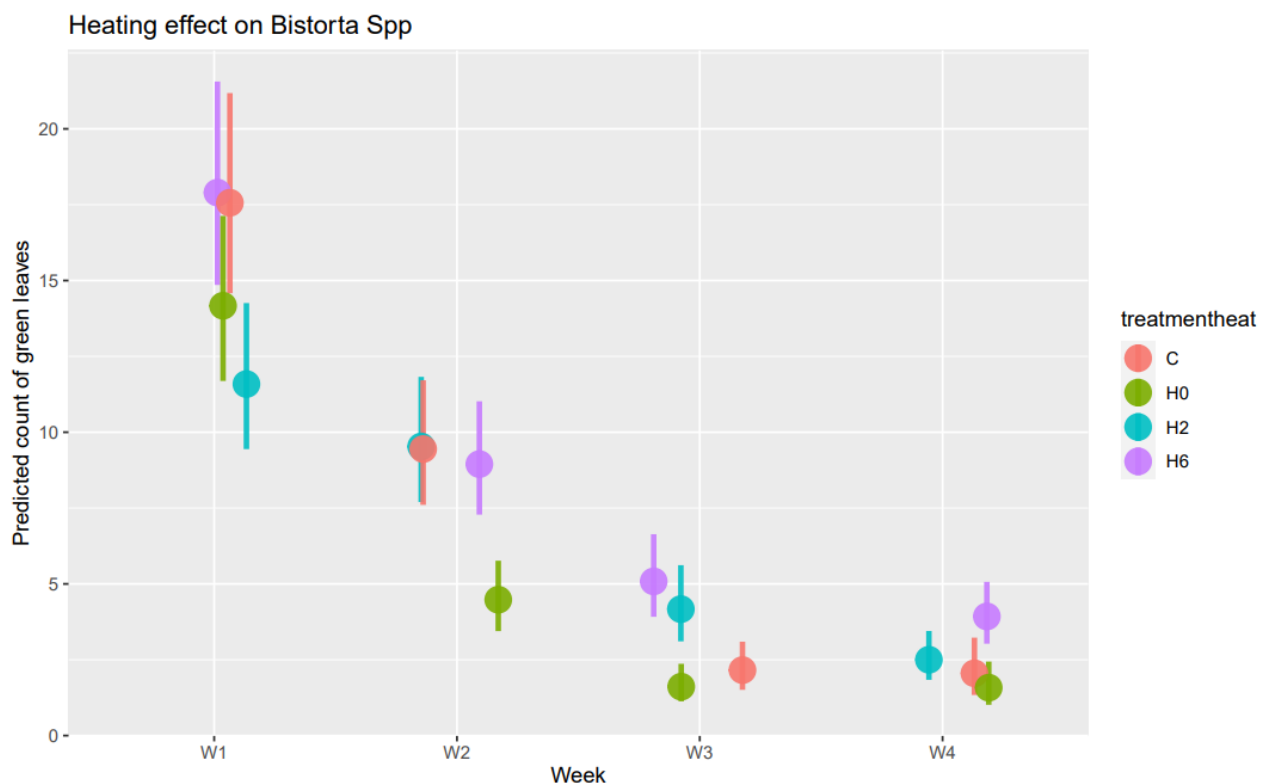


Figure 6: Heating effect on *Bistorta vivipara*. Moisture treatment was removed during the model selection as it did not seem to affect the trajectory of the senescence in *Bistorta*. The figure shows a significant difference between the H6 and the control at week 4. There is no significant difference between H2 and H0 from the control.

3.2.2 *Alopecurus borealis*

The initial proportion of green leaves per pot was variable even before the treatments commenced, with H2 and control pots exhibiting the highest, almost 100%, proportion of green leaves. H6 and H0 treatment pots had about 80% of green leaves (Fig. 7). The interaction between week and the two types of treatment and between the two treatments themselves could inform on the effect of the treatments. The final model (model alin2; Table 2, Table 6 in the appendices) included the interaction between heat treatment and week, moisture treatment and week, and moisture and heat treatments. Towards week two, the treatment effect was not observable as there were over 75% of green leaves in the H2 treatments. The H6 treatments dropped to about 50%, like the zero and control pots. The proportion of green leaves drops further at week three and stays steady at week four for the H6 pots as the H2 treatments' proportion of green leaves drops further towards 50%.

The drop continues in week five and stays steady through to week 7 for the H6 pots, while the H2 pots' proportion of green drops further toward the H0 pots and the control.

Senescence is delayed more in the wet treatments from week four, where there's a clear difference between the proportion of green for the warmest temperature treatment. The H6 wet treatments have about 63% proportion of green while the H6 wet treatments have about 38%. The H6 wet pots have about 35% greenness from week five and the H6 dry treatments have just below 25% proportion of green. The other treatments are similar to the control at just about 10% greenness. At week seven, the proportion of green is basically at 0 apart from H6 pots with 40% at the end of the treatment (Fig.7).

Table 2: A generalized linear mixed model fit by maximum likelihood of the family Binomial for *Alopecurus borealis*. The final model is a generalized linear mixed model fit by the maximum likelihood of the family binomial because the response was a probability. Potid was fit as a random effect. The final model showed a significance for the interaction between the moisture treatment and heat treatment, moisture treatment and week, as well as heat treatment and week. The week here is used as a numeric factor (week2) at $p < 0.05$.

a1lin<- glmer(greencat~treatmentheat*treatmentmoist*week2+scale(shootlength)+(1 potid), data=alo, family=binomial)								
a2lin<- greencat ~ treatmentheat + treatmentmoist + week2 + scale(shootlength) + (1 potid) + treatmentheat:treatmentmoist + treatmentheat:week2 + treatmentmoist:week2, data=alo, family=binomial)								
Model	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)
a2lin	15	3854.7	3949.1	-1912.3	3824.7			
a1lin	18	3857.9	3971.2	-1910.9	3821.9	2.7968	3	0.424
a3lin <- greencat ~ treatmentheat + treatmentmoist + week2 + scale(shootlength) + (1 potid) + treatmentheat:week2 + treatmentmoist:week2, data=alo, family=binomial)								
a3lin	12	3862.6	3938.1	-1919.3	3838.6			
a2lin	15	3854.7	3949.1	-1912.3	3824.7	13.919	3	0.003017***

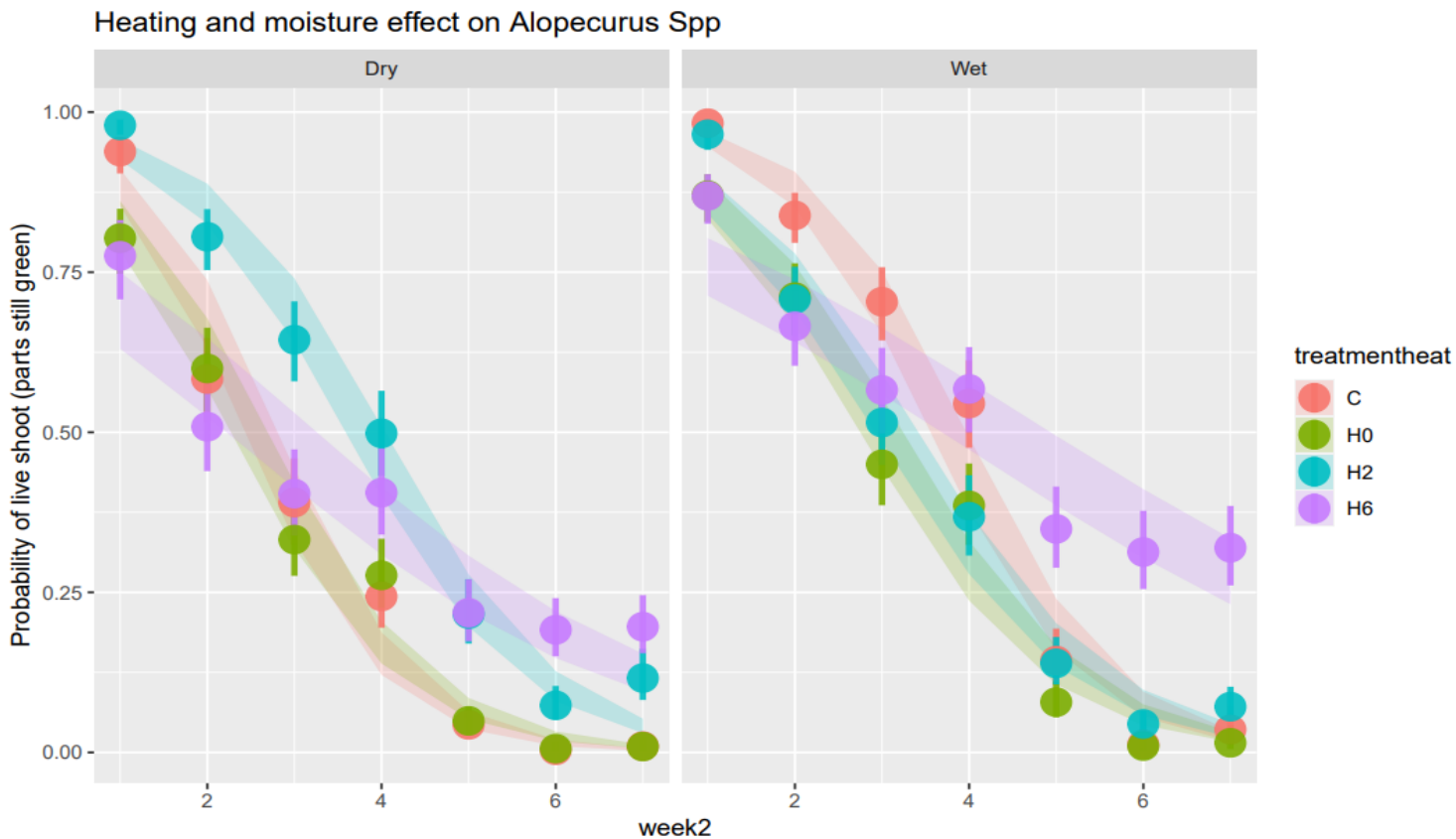


Figure 7: Heating treatment effect on *Alopecurus borealis* leaves. The H6 treatment was significantly different from the control and even more so for the moisture-treated pots. The H2 was significantly different in the wet treatments but not in the dry treatments. H0 was not significantly different from the control.

3.2.3 *Salix polaris*

The initial counts of green *Salix* leaves per pot were also quite variable even before the heating experiment. The highest number of green leaves, about 16, were in the H6 dry pots and 18 in the H6 wet pots. H2 and H0 treatment pots had the lowest number of green leaves, with about eight leaves just before the treatments (Fig. 8). Even though the first model with a 3-way interaction showed significance, it was ruled out because the standard error was enormous indicating overparameterization. The final model for *Salix* (s3; Table 3) included an interaction between week and the two types of treatment. As the weeks progressed, all the treatments had a similar predicted number of green leaves by week three and week four with about one to three leaves in each treatment. The count of green leaves consistently reduced to zero green leaves by the end of the 5th week.

Table 3: Stepwise model selection for *Salix polaris*. The final model(s3) is a generalized linear mixed model fit by the maximum likelihood of the family Poisson because the response was leaf count. Potid was fit as a random effect. Even though the S1 model was significant, the standard error was huge and therefore it was considered inappropriate for the data.

s1<-glmer (leafno. green~treatmentheat*treatmentmoist*week+(1 potid), data=sal, family=poisson)								
s2<-glmer (leafno. green~treatmentheat + treatmentmoist + week + (1 potid) +treatmentheat: treatmentmoist + treatmentheat: week + treatmentmoist: week								
Model	npar	AIC	BIC	logLik	deviance	Chisq	Df	Pr(>Chisq)
s2	29	3697.9	3818	-1820	3639.9			
s1	41	3688.2	3858	-1803.1	3606.2	33.675	12	0.0007588***
s3<-glmer (leafno. green~glmer (leafno. green~treatmentheat + treatmentmoist + week + (1 potid) + treatmentheat: week + treatmentmoist: week								
s3	26	3693.3	3800.9	-1820.6	3641.3			
s2	29	3697.9	3818	-1820	3639.9	1.3759	3	0.7112
s4	14	3723.6	3781.6	-1847.8	3695.6			
s3	26	3693.3	3800.9	-1820.6	3641.3	54.322	12	2.393e-07***
s4<-glmer (leafno. green~glmer (leafno. green~treatmentheat + treatmentmoist + week + (1 potid) + treatmentmoist: week								

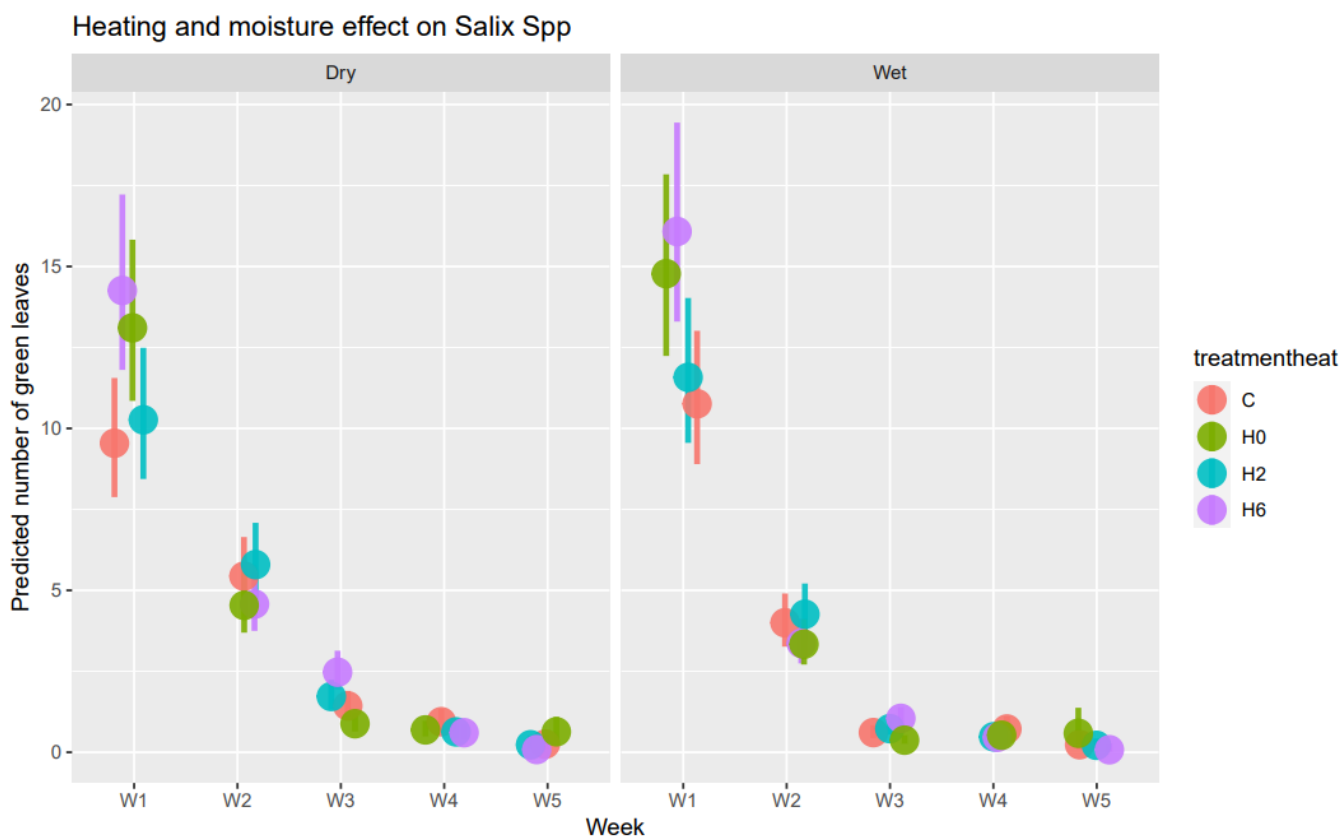


Figure 8: Heating treatment effect on *Salix polaris* leaves. Neither heating nor moisture treatment had an impact on the rate of senescence of *Salix polaris* leaves. The die-off was consistent towards the end of the season.

4 Discussion

My thesis is one of the first studies that have experimentally addressed the predicted climate change effect on the autumn phenology of plants. I found that heat, but not moisture had a substantial impact on delaying senescence in the grass *Alopecurus*, a small effect in the herb *Bistorta*, and no effect in the shrub *Salix*. My findings suggest that delayed senescence of grasses may increase the late-season plane of nutrition for Svalbard reindeer. If *Salix* is representative of Arctic shrubs in general, my results suggest a competitive advantage of grass over shrubs, leading to the speculation that warmer autumns may counteract the predicted shrubification of the Arctic.

4.1 Effect of temperature and moisture on senescence

The autumn heating experiment was able to provide a heating gradient between an average of 2°C to 7°C in the medium (H2) and high (H6) heat treatments, respectively. This temperature increase is relevant and well within the range for many climatic model scenarios stipulated for global warming in the 21st Century; for example, Forland et al., (2011) predict about a 10°C increase in the next 100 years. Hanssen-Bauer et al., (2019) stipulates warmer and wetter autumns that will affect plant responses and, therefore, whole ecosystem disruptions. The report, climate in Svalbard for 2100, shows evidence for an increase in autumn temperature on average of 7.3 – 10.2°C over the next century, suggesting that my temperature manipulation is realistic. There are fewer quantitative predictions for the moisture manipulation, at least for the water available to plants. Overall, with the thawing permafrost in addition to the higher rainfall, the arctic may become even wetter than the projected increase in precipitation would provide alone.

In general, the temperature significantly delayed senescence much more than moisture. A study by (Collins et al., 2021) showed a lengthening of the growing season caused by warming by an average of 1.4°C using OTC. There was a clear advancement of green-up in spring and a delay in senescence in fall, giving an overall longer growing season (+0.8 days) for plants in the tundra on average. Other studies by (Marchand et al., 2004; Zeng et al., 2011) noted a lengthening of the growing season due to climate warming in the arctic. In contrast, previous studies suggest that senescence is controlled by photoperiod but not temperature (Bjorkman et al., 2017; Ernakovich et al., 2014). My study aligns with those finding that increased temperature delays plant senescence.

Moisture, generally, had a lower effect than temperature indicating that precipitation will have a smaller effect on phenology than temperature. A study conducted in a sub-alpine meadow by (Dunne et al., 2003) discovered that soil moisture had minimal effect on temperature-driven phenology response, supported by another study (Rosa et al., 2015) in an Alaskan Tussock Tundra. An experiment by (Collins et al., 2021; Sherry et al., 2007) found that the addition of water did not

affect flowering phenophases in a temperate grassland. My study aligns with research that supports phenology response, more to heat than moisture, at least within the range of treatment levels applied here.

4.2 Differential responses by the study species

There were substantial differences between my representative species in how they responded to treatments. Concerning temperature, the graminoids (*Alopecurus borealis*) (Fig. 5) and the forbs (*Bistorta vivipara*) (Fig. 4) responded with a delayed senescence rate which was more pronounced as the temperature increased. The highest response was experienced in the H6 treatments which are in line with most high emission scenarios from global warming predictions. However, the temperature did not delay senescence in the shrubs (*Salix polaris*) (Fig. 6). Moisture seems to slow the rate of senescence in graminoids (*Alopecurus borealis*) (Fig. 5), but not forbs (*Bistorta vivipara*) (Fig. 4), nor shrubs (*Salix polaris*) (Fig. 6) in this experiment. In a study by (Kremers et al., 2015), graminoids and forbs were the most responsive to climate change drivers as opposed to shrubs. The flowering season was lengthened for graminoids and forbs due to earlier snowmelt in a warming experiment. The result cited is contrary to a study by (Zhu et al., 2012), who discovered a shortened growing period in graminoids caused by warming. A suggestion is that warming causes drying in the soil, which leads to earlier senescence (Oberbauer et al., 2013) and sometimes later initiation of flowering (Dorji et al., 2013), while additional moisture counters this effect. This aligns well with my findings because the most delayed phenology was in watered, hot plots of graminoids.

4.3 Grassification versus shrubification

Several studies have suggested that global warming is leading to the greening of the arctic due to shrubification (Mekonnen et al., 2018; Myers-Smith & Hik, 2018; Myers-Smith et al., 2020; Parker et al., 2021) of the arctic. The reasons cited are mainly temperature and increased moisture regimes in the arctic. However, this is not evident in my study and is supported by (Abbandonato, 2014). The resilience observed in *Salix species*, could be that because their phenology is controlled more by genetics and internal programs (Semenchuk et al., 2016; Zhu et al., 2012). Semenchuk et al., (2016) called such species periodic because they do not alter their phenophases to suit a changing environment. Another reason could be that shrubs are slow growers and therefore have a lesser need for nutrient accumulation during this shortened growing season in the arctic (Chapin et al., 1980), and they will store their reserved nutrients for the subsequent year of growth. Therefore, this lesser need for nutrients means that such species may have a limited response to a changing climate (Tolvanen & Henry, 2001).

In contrast, my analysis finds that warmer autumns may give grass a competitive advantage with the more extended growing season, which may in turn help counteract shrubification. A previous study showed that *Alopecurus species* had enhanced growth under open-top chambers (Abbandonato, 2014; Cooper et al., 2006), reinforced by higher temperature and moisture. Slow-growing species such as *Salix* species may then be predisposed to maladaptation to the changing environment and risk being outcompeted by their more plastic neighbours such as forbs and graminoids (Kremers et al., 2015). Shrubs may not be able to optimize the benefits of a warming and wetter arctic to maximize productivity and maybe outcompeted by other species that do, leading to lower reproductive success for shrubs and higher success for grasses and even forbs.

4.4 Implications for the Svalbard Reindeer

Changes in the phenology of arctic plant species will greatly affect the whole ecosystem including herbivores (Doiron et al., 2015; Ekholm et al., 2022; Kerby & Post, 2013; Tveraa et al., 2013). Gustine et al., (2017) discuss the evidence for trophic mismatches for herbivores in the arctic. Capital breeders, such as the Svalbard reindeer, seem to be more plastic to the changing phenology and show more behavioural advancement to accommodate changes in their life history (Gustine et al., 2017). They seem to postpone reproduction to more favourable conditions to ensure the allocation of more energy to survival rather than reproduction. Income breeders then may be predisposed to trophic mismatches because they rely on current forage abundance for their reproduction and, therefore, may find it hard to change their life history events to a more favourable timing for resources (Gustine et al., 2017).

An animal's body mass is an indicator of resource availability and optimization (Albon et al., 2017; Doiron et al., 2015; Veiberg et al., 2017), which is affected by the locational weather fluctuations, other density-independent and dependent factors. The changing climate, resource availability, and seasonality will play a huge role in informing the effects of global warming in the arctic (Tveraa et al., 2013). As Visser & Both (2005) note, if the phenology of a species is in a different direction or rate to the species that serves as its primary resource (food), then a trophic mismatch is likely to occur from mistiming of events which is why adaptation is key in such ecosystems. The altered seasonality of food resources is likely the most important link between global warming and the future population trajectory of the Svalbard reindeer (Loe et al., 2021), where my study has contributed with new knowledge.

Research shows that arctic sedges such as graminoids respond to grazing by quick regrowth (Chapin, 1980) after herbivory. The following shoots also have higher nutrients than the previously grazed and non-grazed shoots because the demand ensures the allocation of resources to the new

regrowth. Herbivory also prevents the transfer of nutrients to storage organs, unlike in shrubs. Therefore, the higher availability of grasses towards the end of the growing season could mean that reindeer have access to higher sources of nutrients and hence prepare them better for winter survival.

4.5 Limitations

One of the limitations of my study could be delayed or lagged effects. Sometimes, the response to climate change will take years to be observable due to the differential plasticity of species (Collins et al., 2021). It is possible that the *Salix polaris* species, being a long-lived plant species with most of the biomass below ground, could be an example of a plant species showing delayed effects to warming. *Salix species* are also known to use resources accumulated from previous seasons to keep growth and reproduction ongoing, and therefore the current impacts of climate change may go undetected (Collins et al., 2021). More time is required to establish if there were some lagged effects in my study.

My study picked one species from each growth form presented herein: graminoids, forbs and shrubs for representation purposes. However, it is crucial to note that even though plants may represent the same growth form, species within similar growth forms may present different responses to climate change. It is important to note that my study gives an insight into the species but may not be representative for all other species within similar growth forms.

There was an unfortunate difference in the starting values in my experiment. Even though we sampled and potted vegetation from seemingly the same community and visually very similar, there was a difference in the means across treatments already before the treatments started. However, this difference in starting values is unlikely to have affected the significance of senescence rates (interactions between week and treatment), suggesting that I can safely conclude on the differential rates of heat effects and the lower impact of moisture for the plant species evaluated in my study.

5 Conclusion and future perspective

My study, using a representative species from three forage species for the Svalbard reindeer, was able to show that adding a heat load compatible to moderate climate predictions resulted in a substantial delay in senescence of grass. Recent research has concluded that warmer autumns have more than offset the effect of icier winters over the last 25-year period (Loe et al., 2021). The mechanism of this autumn effect remains unclear but has been linked to onset of snow. It is possible that one of the mechanisms for the positive autumn effect is that the reindeer can feed on green higher quality vegetation for longer and enter the winter season with larger fat reserves. Therefore, my study begins a journey towards understanding the link between the increasing reindeer body mass and population in connection to food availability in the autumn.

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7 Appendices

Table S1: A summary of the best-fit model for the *Bistorta vivipara* species. A generalized Linear Mixed Model showing the significance levels for the different variables and their *p* values.

bispo5 <- glmer (leafno ~ treatmentheat+ week + (1 potid) +treatmentheat: week, data=bis. green. count, family=Poisson)					
	AIC	BIC	logLik	deviance	df. Resid
	448.2	488.3	-207.1	414.2	61
Scaled residuals:	Min	1Q	Median	3Q	Max
	-2.143	-0.7307	-0.1917	0.5857	3.066
Fixed effects:	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	2.86583	0.18667	15.353	< 2e-16 ***	
treatmentheatH0	-0.2158	0.26725	-0.808	0.41937	
treatmentheatH2	-0.4155	0.27795	-1.495	0.134937	
treatmentheatH6	0.0188	0.26274	0.072	0.942962	
weekW2	-0.62	0.16542	-3.748	0.000178 ***	
weekW3	-2.0973	0.33127	-6.331	2.43e-10 ***	
weekW4	-2.1397	0.42432	-5.043	4.59e-07 ***	
treatmentheatH0:weekW2	-0.5352	0.28041	-1.908	0.056333.	
treatmentheatH2:weekW2	0.42387	0.25315	1.674	0.094061.	
treatmentheatH6:weekW2	-0.0732	0.23115	-0.317	0.751619	
treatmentheatH0:weekW3	-0.068	0.48087	2.476	0.036351 *	
treatmentheatH2:weekW3	1.07791	0.43527	2.476	0.013271 *	
treatmentheatH6:weekW3	0.84028	0.40147	2.093	0.036351 *	
treatmentheatH0:weekW4	-0.058	0.59996	-0.097	0.92297	
treatmentheatH2:weekW4	0.61232	0.5184	1.181	0.237535	
treatmentheatH6:weekW4	0.62229	0.47786	1.302	0.192835	
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					

Table S2: A summary of the best-fit model for the *Salix polaris* species. A generalized Linear Mixed Model showing the significance levels for the different variables and their p values.

s3<-glmer (leafno. green~glmer (leafno. green~treatmentheat + treatmentmoist + week + (1 potid) + treatmentheat: week + treatmentmoist: week, data=sal, family=Poisson)					
	AIC	BIC	logLik	deviance	df. Resid
	2555.4	2614.3	-1261.7	2523.4	278
Scaled residuals:	Min	1Q	Median	3Q	Max
	-5.0268	-1.0233	-0.1065	1.1808	5.811
Fixed effects:	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	2.29069	0.1671	13.709	< 2e-16 ***	
treatmentheatH0	0.30999	0.20776	1.492	0.1357	
treatmentheatH2	0.17665	0.21492	0.822	0.4111	
treatmentheatH6	0.39253	0.20844	1.883	0.0597.	
treatmentmoistWet	0.08395	0.14915	0.563	0.5735	
weekW3	-1.8993	0.21967	-8.646	< 2e-16 ***	
weekW4	-2.3109	0.3079	-7.505	6.13e-14 ***	
treatmentheatH0:weekW3	-0.8198	0.33079	-2.478	0.0132 *	
treatmentheatH2:weekW3	0.06088	0.28027	0.217	0.828	
treatmentheatH6:weekW3	0.15131	0.26069	0.58	0.5616	
treatmentheatH0:weekW4	-0.6394	0.40932	-1.562	0.1183	
treatmentheatH2:weekW4	-0.5292	0.43717	-1.921	0.0548	
treatmentheatH6:weekW4	-0.8396	0.43717	-1.921	0.0548.	
treatmentmoistWet: weekW3	-0.9516	0.21126	-4.504	6.66e-06 ***	
treatmentmoistWet: weekW4	-0.3547	0.33117	-1.071	0.2842	
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					

Table S3: The best fit model summary for the *Alopecurus borealis* species, using the week as a numeric factor. Fit by generalized Mixed Linear Model with maximum likelihood ratio, of the family binomial.

a2lin<- greencat ~ treatmentheat + treatmentmoist + week2 + scale(shootlength) + (1 potid) + treatmentheat: treatmentmoist + treatmentheat: week2 + treatmentmoist: week2, data=alo, family=binomial)					
	AIC	BIC	logLik	deviance	df. Resid
	3854.7	3949.1	-1912.3	3824.7	3989
Scaled residuals:	Min	1Q	Median	3Q	Max
	-7.8228	-0.5623	-0.1714	0.6039	9.8029
Fixed effects:	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	3.2987	0.32713	10.085	< 2e-16 ***	
treatmentheatH0	-0.69039	0.42923	-1.608	0.10774	
treatmentheatH2	0.51521	0.44939	1.146	0.25161	
treatmentheatH6	-2.01792	0.41983	-4.806	1.54e-06 ***	
treatmentmoistWet	1.00022	0.37668	2.655	0.00792 **	
week2	-1.2557	0.0805	-15.6	< 2e-16 ***	
scale(shootlength)	-0.51209	0.04377	-11.701	< 2e-16 ***	
treatmentheatH0: treatmentmoistWet	-0.80518	0.45582	-1.766	0.07732.	
treatmentheatH2: treatmentmoistWet	-2.0079	0.46076	-4.358	1.31e-05 ***	
treatmentheatH6: treatmentmoistWet	-0.77184	0.46307	-1.667	0.09556.	
treatmentheatH0: week2	0.20592	0.0963	2.138	0.03249 *	
treatmentheatH2: week2	0.25651	0.09255	2.772	0.00558 **	
treatmentheatH6: week2	0.7908	0.08123	9.736	< 2e-16 ***	
treatmentmoistWet: week2	0.11434	0.05482	2.086	0.03702 *	
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					



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