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The effects of increased soil moisture on the timing of senescence of three plants grazed by Svalbard reindeer

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Master of Science in Natural Resource Management

Preface

This 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, under the Norwegian University of Life Sciences (NMBU).

I would like to give a big thank you to my supervisor, Professor Leif Egil Loe, for all of his help and support, as well as for the opportunity to take part in this project and conduct field work on Svalbard. I would also like to thank Samantha Dwinnell and René van der Wal for their help and input both during field work and writing.

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

Abstract

Climate change is affecting the Arctic faster than anywhere else on the planet, with increases in temperature and precipitation predicted to have significant effects on Arctic ecosystems. Water availability is of key importance to plant growth in the Arctic, and the availability of grazing in the autumn is of particular importance to the winter survival of Arctic herbivores. Despite this, the effects of water availability on the senescence of plants in the Arctic is largely understudied. I experimentally tested how different levels of soil moisture impacted the senescence of a grass, an herb, and a shrub all commonly found on Svalbard, that are also important to the grazing of Svalbard reindeer. Increased soil moisture had a strong positive effect by delaying the timing of senescence of the grass in particular. Meanwhile, senescence was delayed for the herb and forb only under moderate increases in soil moisture, while high increases in soil moisture led to earlier senescence. Flooding events caused by heavy rainfall may have a strong negative impact on some species, such as the herb and forb, while species like the grass may be more resilient. These results indicate that a moderate increase in precipitation in the future may have a positive effect on the length of time with high quality forage available during the autumn, which may ameliorate the negative effects expected from increased icing events during the winter on Arctic herbivores such as the Svalbard reindeer.

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1 Introduction

The Arctic is experiencing climate change faster than the Northern Hemisphere in general, with loss of sea ice and increasing moisture being key contributors to rising temperatures (Box et al., 2019). Over the past decades many parts of the Arctic have also been 'greening', with increasing vegetation indices and plant productivity connected to land warming (Bhatt et al., 2010; Elmendorf et al., 2012; Myers-Smith et al., 2020). The growing season is lengthening across the northern hemisphere, with earlier onset of spring and a later end of autumn (Park et al., 2016), yet autumn remains an understudied season in climate change research (Gallinat et al., 2015). High Arctic plants are particularly sensitive in terms of phenological timing, and changes in temperature and snow cover can affect flowering, greening, and senescence (Oberbauer et al., 2013). Both the onset and the rate of senescence can be affected by air temperature, with soil moisture and soil temperature being contributing factors (Livensperger et al., 2019). Any changes in vegetation composition and phenology will affect the grazing species dependent on them, making the directionality of plant species response to climate change important to understand.

Some of the factors connected to climate change currently impacting reindeer across the northern hemisphere are altered plant community compositions, new disease patterns, increased icing events, and longer and more productive growing seasons (Mallory & Boyce, 2018). The timing of seasons can have a significant impact on plant phenology with cascading effects on herbivores. In Idaho, a study on mule deer found that the effects of a longer, more productive autumn had a stronger effect on fawn body mass and survival than spring did (Hurley et al., 2014). Changes in conditions have already been shown to impact large herbivores in the Arctic as well, ranging from increased habitat suitability to increased mortality from extreme weather events such as rain-on-snow, which can block access to food in winter (Hansen et al., 2014; van Beest et al., 2023). An earlier onset of spring has been shown to cause a mismatch with calving in caribou and optimal forage timing (Post & Forchhammer, 2008). In general, the winter season has large effects on survival with subsequent fitness consequences for the following spring and summer (Williams et al., 2015). The possibility for additional body mass build-up during the autumn season is therefore of key importance for populations of large herbivores in the Arctic.

Plant response to climate change is not equal across the Arctic or even across the landscape, and there may be variation according to soil moisture, canopy height, and geographic location (Myers-Smith et al., 2015). With the Arctic having a growing season typically spanning only

two to three months (Le Moullec et al., 2019), the timing of autumn senescence is of particular importance not only to maximize plant growth, but also to ensure proper resorption and development of frost hardiness (Gehrmann et al., 2022). Studies have shown varying results on the effects of temperature on senescence, with some finding evidence that higher temperatures delayed senescence (Collins et al., 2021; Marchand et al., 2004; May et al., 2017) and others showing earlier senescence or species specific responses, which may be connected to water limitations (Gehrmann et al., 2022; Livensperger et al., 2019; Oberbauer et al., 2013). Many tundra vascular plants are adapted to a wider range of water conditions and are typically stronger competitors than mosses and lichens, but under too dry or too wet conditions the opposite may also be true (Kemppinen et al., 2019). The directional effects of water availability on plant growth may therefore be both species specific and dependent on water quantity. Despite soil moisture being an important factor in determining climate sensitivity of growth and senescence in the Arctic (Livensperger et al., 2019; Myers-Smith et al., 2015), few studies have focused on the more isolated effects of different soil moisture levels.

Along with the rest of the Arctic, the archipelago of Svalbard has been experiencing increasing temperatures and hydrological changes. Under medium to high predicted climate change scenarios, Svalbard is expected to face higher temperatures, more precipitation, shorter snow seasons, and more frequent extreme weather events (Hanssen-Bauer et al., 2019). The number of growing days on Svalbard is predicted to increase by 3-4 times the current observations by 2100, while the amount of rainfall is predicted to increase especially in the autumn, with subsequent increases in rain-flood events (Hanssen-Bauer et al., 2019). Such changes in hydrology can have a large impact on the plant communities on the tundra, as species have different optimum growing conditions favored by either wetting or drying (Hodkinson et al., 1999). Moss-dominated tundra helps to retain moisture and keep the tundra cool, but current climate projections seem to favor a shift towards a more herbaceous state with herbs growing in a moss matrix, which has warmer soils and a deeper active layer (Ravolainen et al., 2020). Svalbard has very limited vegetation cover, with only ca. 170 different plant species (Thuesen & Barr, 2022). Some species, such as the polar foxtail (*Alopecurus ovatus*), alpine bistort (*Bistorta vivipara*), and polar willow (*Salix polaris*) have all increased in occurrence frequency in Svalbard over the past few decades (Kapfer & Grytnes, 2017). There is evidence that there is a positive effect of summer temperatures on the aboveground biomass of multiple vascular plants in the High Arctic (René Van Der Wal &

Stien, 2014), as well as a delay in senescence (Collins et al., 2021). Such changes in climate and plant communities will also affect higher trophic levels, with warmer summers positively related to plant biomass (René Van Der Wal & Stien, 2014).

With low hunting pressure and no natural predators, the Svalbard reindeer (*Rangifer tarandus platyrhynchus*) are largely regulated bottom-up through food availability. Reindeer also affect the landscape in return through grazing and trampling, encouraging the growth of forbs and herbs (R. Van Der Wal & Brooker, 2004). This feedback loop can thus enhance the changes that the Arctic tundra is already experiencing, such as the Arctic greening seen in varying degrees throughout the Northern Hemisphere (Berner et al., 2020). Winter climate is a well-known predictor for population size in reindeer (Aanes et al., 2000; Albon et al., 2017; Solberg et al., 2001), yet the effects of autumn are much less studied despite the length of the growing season being a key factor in determining how well prepared the animals are to face the long winter. A longer growing season due to warmer autumns and a longer snow-free period can have cascading effects on the late winter body mass of Svalbard reindeer as it allows for increased energy intake and reduced winter mortality (Loe et al., 2021). With detrimental events such as icing from rain-on-snow expected to increase in frequency (Hanssen-Bauer et al., 2019), the opportunity to build up body mass reserves can become of key importance to the survival of reindeer populations in the Arctic (Tews et al., 2007).

In this study I aim to investigate the effects of increased soil moisture on the growth of three plant species common on the Arctic tundra on Svalbard that are also favored grazing species of the Svalbard reindeer: *Alopecurus ovatus*, *Bistorta vivipara*, and *Salix polaris*. By altering the water availability of the plants in a replicated field experiment I will test whether increased soil moisture will lead to delayed leaf senescence and therefore extend the growing season and time period with high quality forage in Svalbard, as well as how the effect may differ between the plant species.

2 Materials and Method

2.1 Study area

Fieldwork was conducted from July to September 2022 in Adventdalen, Svalbard (78.20°N;15.81°E). The valley has a width of ca. 3.5-4 kilometers, and the river Adventelva runs through to create a large wetland area where it meets Adventfjorden (Barr, 2021). The area belongs to the phytogeographical zone middle Arctic tundra (MATZ), and is especially rich in moss-tundra and wetlands, and many areas are strongly affected by flooding (Johansen et al., 2009; Norsk polarinstitutt, 2022). In July to September, the average temperature for the area is ca. 5°C and average total precipitation is 23.3 mm. In 2022, temperatures and precipitation were slightly above average at 6.5°C and 24.4 mm, respectively. August was considerably wetter than normal, however, with a total precipitation of 41.5 mm compared to the typical 23 mm (Yr.no, n.d.).

Figure 1: Map showing study site location, at approximately 78.20°N;15.81°E. The map was made in QGIS with map data provided by the Norwegian Polar Institute (Norsk polarinstitutt, 2020).

2.2 Study species

Alopecurus ovatus is a perennial, moisture dependent grass found mainly in Arctic, mountain, flood, coastal, and wetland habitats and is common throughout Svalbard and Bjørnøya

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(Solstad et al., 2021b). Aerial shoots grow from branched rhizomes, and leaves are typically 5-10 cm long while the culm is typically 7-25 cm long (Svalbardflora, 2020a). *Salix polaris* is a small perennial shrub and one of the most common plants on Svalbard, growing mainly in Arctic, alpine, flood, coastal, wetland, and rocky habitats (Solstad et al., 2021c). It forms extensive mats with its branched stems, and is particularly dominant in snow-beds. The shoots typically reach 1-3 cm in height, with alternating rounded leaves ca. 1.5 cm long and wide (Svalbardflora, 2020c). *Bistorta vivipara* is a perennial herb also common throughout Svalbard in dry to moist soils, with its main habitats being Arctic, alpine, rocky, flood zones, and coastal areas (Solstad et al., 2021a). Plants may have one or several stems growing from a rhizome, with alternating leaves ca. 2-5 cm long (Svalbardflora, 2020b).

These three species are some of the most important foraging species of the Svalbard reindeer, particularly during the summer, though *S. polaris* is also favored during the winter (Bjørkvoll et al., 2009).

2.3 Experimental study design and data collection

Five blocks were identified and established between July 25th and July 27th 2022. Each block contained three 40x40 cm square plots within 1-3 meters of each other that received different treatments, and were called "wet", "dry", and "control" (figure 2). This left a total of 15 plots with five replicates for each treatment. To establish the plots, squares were measured out with a ruler and a bread knife was used to cut about 15 cm into the ground. A spade was then used to lift the turf. For the "control" plots the turf was simply dug out and lifted up before being placed back into the ground. For both the "wet" and "dry" plots a waterproof plastic sheet was placed down in the hole, large enough to cover both the bottom and the sides, before the turf was placed back into the ground. The purpose of the plastic layer between the plots and the ground was to prevent water from the surrounding area to enter or exit the plots, making it easier to control the moisture level.

To maintain a higher moisture level in the wet plots, they were watered with 2 liters after being fully established, complete with marked shoots of *A. ovatus* and *B. vivipara*. Neither the dry plots nor the control plots were manually watered, and only received water from rainfall and (in the case of the control plots) lateral water movement from the surrounding tundra. Due to exceptionally heavy rainfall the summer/autumn of 2022, the wet plots received varying amount of manual watering throughout the experimental period in an attempt to keep the moisture level stable. Originally the wet plots were to be watered with 4 liters twice

weekly (Tuesday and Thursday). This system had to be abandoned early as rainfall added excess water to the plots and caused some of them to be almost entirely submerged (See S7 for an example). Instead the plots were monitored visually and watered when the water level sank again. The final watering schedule can be seen in table 1. To measure soil moisture and temperature a TOMST TMS-4 datalogger was placed in each plot August 8th when measurements started, and were removed September 25th along with the rest of the equipment. The loggers have three sensors that measure temperature at approx. 15 cm, 0 cm, and -6 cm relative to the ground surface. The moisture sensor uses the time-domain transmission (TDT) method and measures approx. 0-14 cm below ground surface, with a numerical range of 1-4095 in raw TDT data where 3500 is about equal to distilled water (Wild et al., 2019). Calibrating the TDT raw data to volumetric soil moisture was not within the scope of this thesis, and so the TDT raw data is presented instead.

The data was collected over a period of seven weeks, from August 8th to September 22nd 2022, and the method varied slightly for each of the three species.

2.3.1 Alopecurus ovatus

In each plot five shoots of *A. ovatus* visually considered "large" and five shoots visually considered "small" were picked out, resulting in a total of ten *A. ovatus* shoots per plot that were to be observed and measured over the course of the experiment. Each shoot was marked with a thin strand of colored yarn tied around the base so they could be easily reidentified. Large and small shoots were marked with different colored yarn, and beyond this individual shoots were recognized based on spatial location within each plot. For each measurement the date, shoot ID, block, treatment, yarn color (i.e. size), shoot number, blade number, and percentage of greenness for each blade was noted. Additionally, during the first measurement the length of each blade was also measured.

2.3.2 Salix polaris

Due to the large number of *S. polaris* leaves a 10x10 cm square within each plot was identified for *S. polaris* measurements. A removable measuring square was made by sawing and gluing birch "pinnekjøttpinner" together, and then cotton string was used to create a 2x2 grid within the square to make measurements easier. Four toothpicks were permanently placed in each plot at the corners where the birch square was to be laid down in order to measure the same spot every time. *S. polaris* leaves were then measured within the 10x10 square, using the string grid to focus on four smaller areas at a time. For each measurement the date, block, treatment, and the number of *S. polaris* leaves of different colors (green,

yellow, red, or brown) were recorded. Leaves were included in counts as long as they remained attached to the ground.

2.3.3 Bistorta vivipara

A minimum of ten and a maximum of 18 *B. vivipara* leaves per plot were initially chosen at random and marked with a toothpick next to them. The top of the toothpick was colored with black marker to make them easier to spot and separate them from the toothpicks marking the placement for the measuring grid for *S. polaris*. As the number of *B. vivipara* leaves were generally low within the plots the risk of bias when choosing plants to track is likely low as it was often difficult to find ten *B. vivipara* leaves at all, resulting in a variety of leaf sizes in each plot. Unlike for the *A. ovatus*, the *B. vivipara* leaves did not have unique IDs, so the order they were measured in varied. For each measurement, the date, block, treatment, plant number, and color of the leaf (green, yellow, red, or brown) was noted. Leaves were recorded as long as they remained attached to the ground.

Table 1: Watering schedule for "wet" plots 2022.

Date (day/month)	Amount watered
26/7 – 27/7	2 liters
29/7	4 liters
02/8	4 liters
05/8	4 liters
12/8	1 liter

In total, the data contains information from a total of 150 shoots of *A. ovatus*, which were followed at an individual level where all shoots were identifiable until the end. There were initially 168 leaves of *B. vivipara* identified, however a few leaves were lost over time and so the final count was of a total of 153 leaves. Due to the large number of *S. polaris* leaves they were not followed at an individual level, and rather every leaf observed within the measuring area was counted each time. This lead to a total of 8059 counts of *S. polaris* leaves by the end of the experiment. Due to snow cover, data in week 37 could only be collected for one block (See S8 for an example of a snow-covered plot). At the end of the experimental period all yarn, toothpicks, and plastic was removed from the tundra and brought back for storage or recycling.
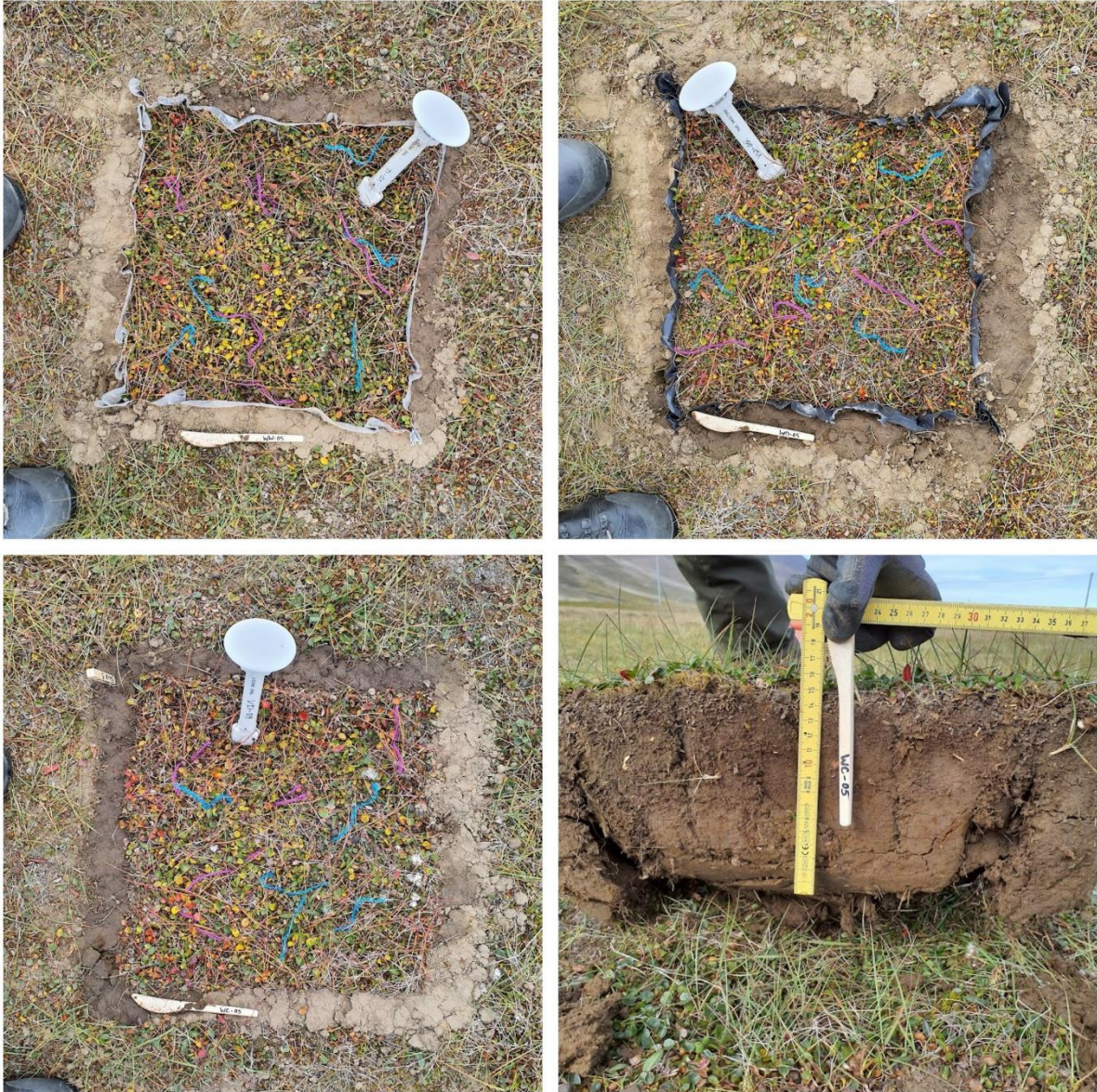
Figure 2: Photos of block 5. Wet treatment is the upper left photo, intermediate treatment is upper right photo, control is bottom left photo, and a soil profile of the control is the bottom right photo. *A. ovatus* shoots have been marked as "large" with purple yarn and "small" with blue yarn. Temperature and moisture was recorded in each plot with a TMS-4 datalogger.
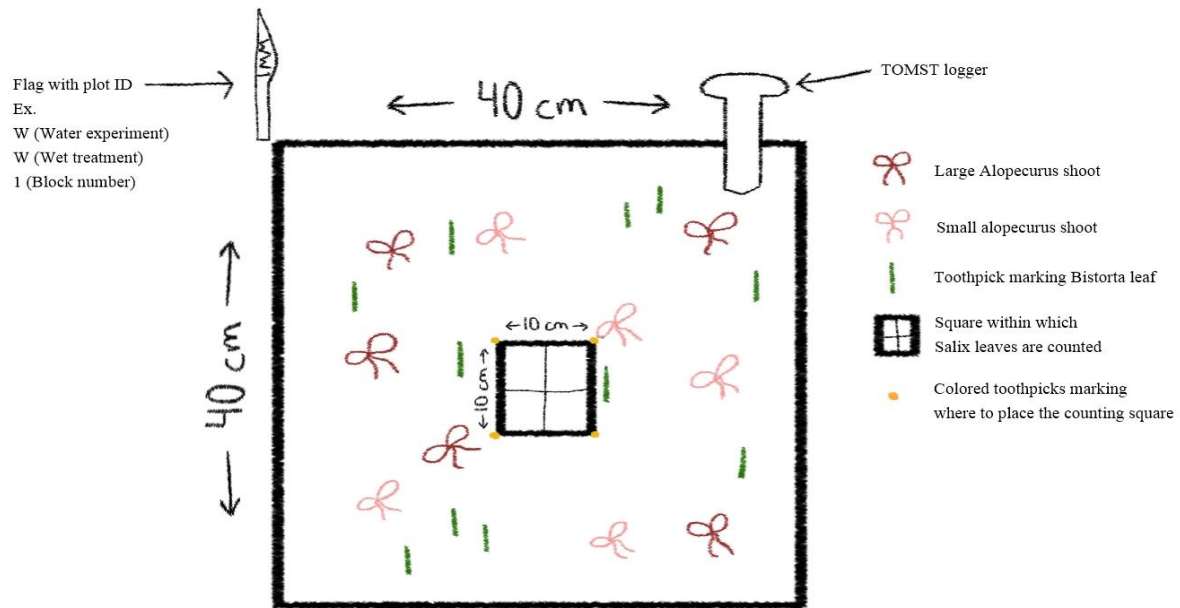
Figure 3: Sketch of plot set-up of watering experiment in Adventdalen. Each plot contained five large and five small shoots of *A. ovatus*, ten toothpicks marking *B. vivipara* leaves, four colored toothpicks marking where to place the measuring grid for *S. polaris*, and one TMS-4 datalogger. The measuring square itself is removable so it could be reused for each plot.

2.4 Statistical analysis

Data handling was done in Microsoft excel and RStudio Version 1.4.1717 (RStudio Team, 2021) in the tidyverse package (Wickham et al., 2019). Statistical analysis was also done using RStudio Version 1.4.1717.

For *A. ovatus*, the proportion of a leaf being green was used as a response variable while date, treatment, and their interaction were used as explanatory variables in a generalized linear mixed-effect model (GLMM). Individual leaf within blocks was fitted as nested random effects and errors were assumed to be binomially distributed.

For *S. polaris*, a GLMM was fitted using number of live leaves as a Poisson distributed response variable. Week and treatment were both factor variables, and their interaction was fitted as predictor variables. Leaves were considered alive if they had been recorded as green, yellow, or red while any brown leaves were considered dead. Block was fitted as a random effect, and number of live leaves per plot at first measuring date was used as an offset variable to account for the different starting values in number of leaves per plot.

For *B. vivipara*, the same GLMM as used for *S. polaris* was initially tested, however the model did not converge. As a consequence of this, a generalized linear model was used instead to test for differences in the proportions of live leaves separately by week, in weeks where large visual differences between treatments were observed in the raw data.

To select the best model for *A. ovatus* and *S. polaris*, I ran a backward model selection in the form of Likelihood Ratio Tests (LRT; using the anova function) (Pinheiro & Bates, 2000). If the interaction fell out, the least significant of the main effects of treatment and date was attempted removed until only significant predictor variables remained in the model.

3 Results

3.1 Moisture and temperature

The average daily moisture count was highest for the wet plots (min= 2795, max= 3712, mean= 3517), second highest for the "dry" plots (min= 1433, max= 3329, mean= 2361), and lowest for the control plots (min= 1171, max= 3377, mean= 2130). Thus, the dry plots ended up retaining too much water and had a higher average moisture level than the control plots, and will henceforth be referred to as an intermediate treatment. In addition, the moisture level was the most stable for the wet plots across all blocks, but varied for the intermediate and control plots (Fig. 4). The intermediate plot of block 2 had a lower and more stable moisture level than the other intermediate plots, while the control plot of block 5 was noticeably drier than the rest of the control plots.
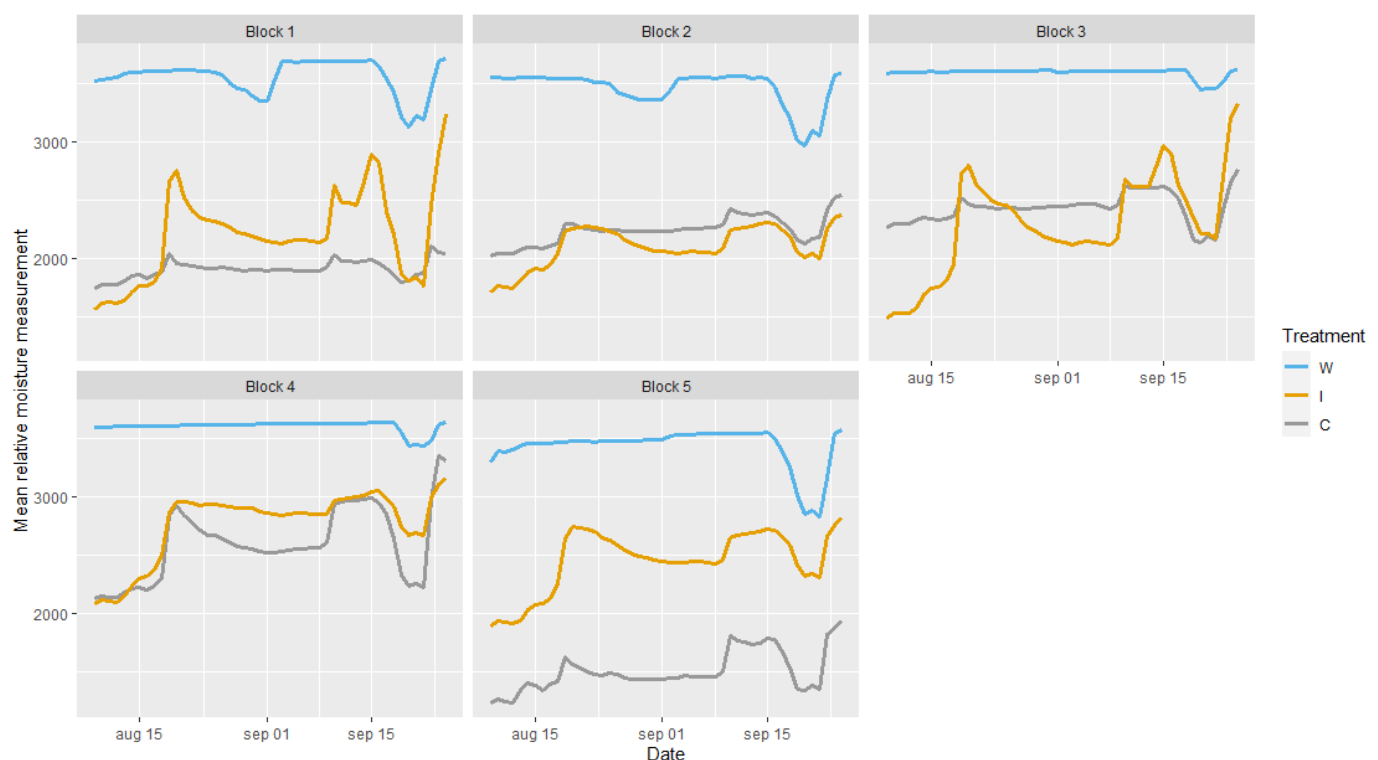

Figure 4: Daily relative moisture measurements for each plot. Wet treatment (W) represented with blue lines, intermediate treatment (I) represented with orange lines, and control treatment (C) represented with gray lines.

There was a sharp increase in moisture count for both the control and intermediate plots around mid to late August (approx. August 19[th)], following a period of heavy rainfall between August 18th-20th. The moisture level slowly sank a little before spiking again early to mid-September. This coincides with another period with precipitation as rain and snow between September 10th-13th. The final spike at the end of September coincides with a period of warming and snowmelt. Air temperature (Fig. S11) ranged from -8.3°C to 16.8°C, ground temperature (Fig. S10) had a range of -4.6°C to 16.4°C, and soil temperature (Fig. 5) had a range of -0.2°C to 9.3°C. Soil temperatures were notably more stable than temperature measured at ground level and in the air, and in three blocks the wet treatment at times showed marginally higher soil temperatures compared to the intermediate and control plots.
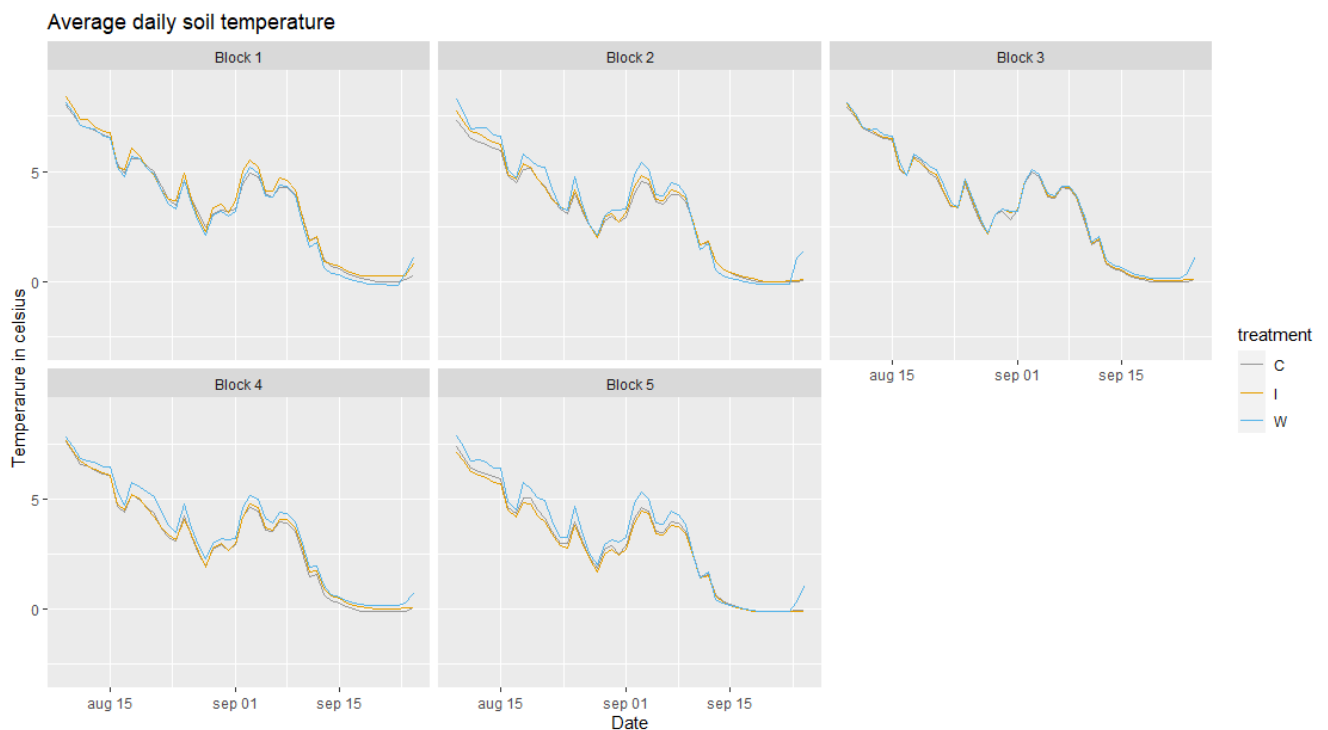

Figure 5: Average daily soil temperature measurements, measured at ca. 8 cm below ground level. Wet treatment (W) represented with blue lines, intermediate treatment (D) represented with orange lines, and control treatment (C) represented with gray lines.

3.2 Alopecurus

Shoots in the intermediate treatments remained greener slightly longer than those in control treatments (Fig. 6). By the end of the experimental period, *A. ovatus* leaves in wet treatment plots were on average more than 50% green, while the corresponding proportions for intermediate and control treatments were less than 25%. The effects of watering seemed clear both when grouped together by treatment (Fig. S1) and when treatment was replaced with soil moisture for each plot (Fig. S2). Model selection supported retaining the interaction between

week and treatments (Likelihood ratio test: p<0.001) with a significantly slower senescence rate in intermediate (p=0.046) and wet (p<0.001) treatments relative to the control (Table 2).

Table 2: Estimates for generalized linear mixed-effect model for *Alopecurus ovatus* summarizing the effects of watering on the proportion of leaves being green throughout the season (August-September). Because the raw data indicate near linear senescence rates in all treatments, week of measurement was treated as a linear variable.

Random effects:

Groups	Name	Variance	Std.Dev.	Corr
id:block	Intercept	4.52E-06	0.0021	
	Week nr.	3.73E-09	0.0001	-1.00
block	Intercept	2.86E-01	0.5346	
	Week nr.	5.88E-04	0.0243	-1.00

Number of obs: 1943, groups: id:block, 150; block, 5

Fixed effects:

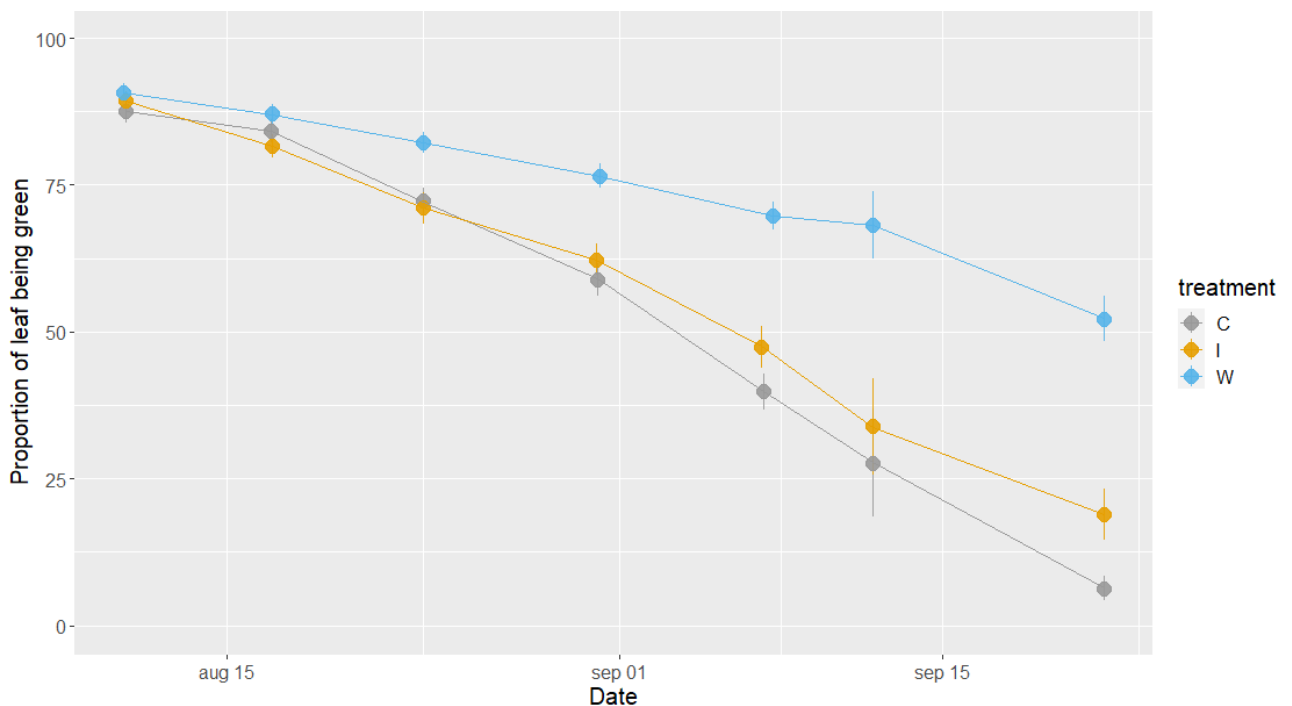|	Estimate	SE	z	p
Intercept	0.671	0.171	3.93	< 0.001
Treatment I	0.225	0.151	1.49	0.136
Treatment W	0.960	0.154	6.24	< 0.001
Week nr. (scaled)	-1.701	0.144	-11.84	< 0.001
Treatment (I vs C)	0.371	0.186	2.00	0.046
Treatment (W vs C) x Week	0.911	0.171	5.32	< 0.001

Figure 6: Raw data plot showing the effects of watering on *Alopecurus ovatus* in 2022 for each treatment. Wet treatment (W) represented with blue lines, intermediate treatment (D) represented with orange lines, and control treatment (C) represented with gray lines.

3.3 Salix

In contrast to *A. ovatus*, the raw data indicates a negative effect of watering on *S. polaris* when grouped by treatment (Fig. S3) as well as when grouped by average soil moisture (Fig. S4). A greater proportion of leaves remained alive further into the season in intermediate (highest proportion) and control (second highest proportion) treatment plots compared to wet (lowest proportion) treatment plots, and a greater average soil moisture caused leaves to wither faster (Fig. 7). The difference in survival between the control and intermediate treatment plots were not large, while plants in the five wet treatment plots died faster than the plants in almost all other treatments. The plot that kept the greatest proportion of live leaves of the longest belonged to an intermediate treatment. By mid to late September almost all plants were predicted to have withered regardless of treatment.

Modelled results corroborate the trends from the raw data, with a significant negative effect of treatment on the length of time that *S. polaris* leaves remained alive (significant interaction between date and treatment; table 3).

Table 3: Estimates for a generalized linear mixed-effect model of *Salix polaris* data summarizing the effects of watering on the number of live leaves throughout the season (August-September). Week is treated as a factor variable in the model. Weeks 36 to 38 had to be combined into one class for the model to converge.

Random effects:

Groups	Name	Variance	Std.Dev.
block	(Intercept)	0.028	0.166

Number of obs: 89, groups: block, 5

Fixed effects:

|	Estimate	SE	z	p
intercept	-0.03	0.08	-0.41	0.685
treatment (I vs C)	0.01	0.05	0.14	0.890
treatment (W vs C)	-0.03	0.05	-0.68	0.494
week 33 (vs 32)	-0.25	0.05	-4.72	< 0.001
week 34 (vs 32)	-0.51	0.06	-8.82	< 0.001
week 35 (vs 32)	-1.23	0.07	-16.61	< 0.001
week 36-38 (vs 32)	-4.17	0.20	-21.30	< 0.001
treatment I:week 33 (vs 32)	0.07	0.08	1.00	0.319
treatment W:week 33 (vs 32)	-0.19	0.08	-2.48	0.013
treatment I:week 34 (vs 32)	0.04	0.08	0.48	0.634
treatment W:week 34 (vs 32)	-0.60	0.09	-6.77	< 0.001
treatment I:week 35 (vs 32)	0.25	0.10	2.48	0.013
treatment W:week 35 (vs 32)	-1.75	0.17	-10.28	< 0.001
treatment I:week 36-38 (vs 32)	0.98	0.23	4.24	< 0.001
treatment W:week 36-38 (vs 32)	-1.82	0.54	-3.38	0.001
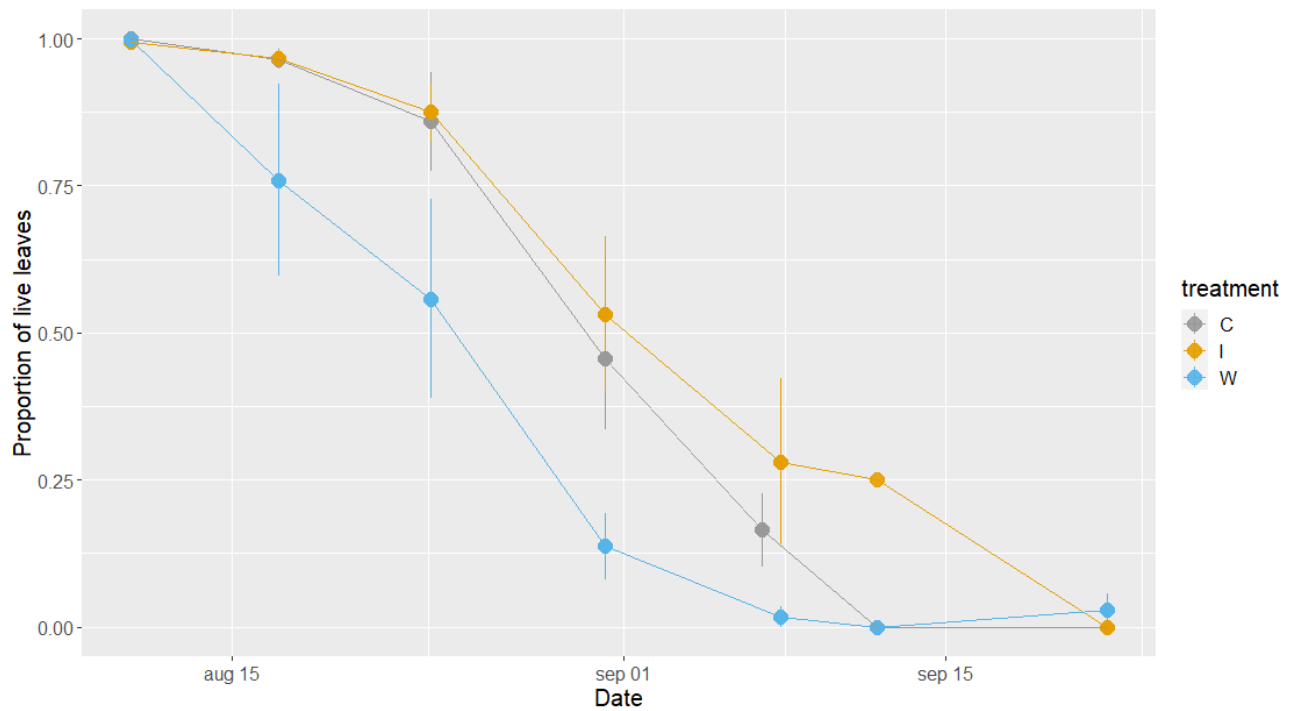
Figure 7: Raw data plot showing the effects of watering on *Salix polaris* in 2022 for each treatment. Wet treatment (W) represented with blue lines, intermediate treatment (D) represented with orange lines, and control treatment (C) represented with gray lines.

3.4 Bistorta

As with *S. polaris*, the raw data indicated a strong negative effect of treatment on *B. vivipara*. There was a greater proportion of live leaves later in the season in intermediate (highest proportion) and control (second highest proportion) plots than in the wet (lowest proportion) plots (Fig. 8). Four out of five wet treatment plots lost leaves faster than all other treatment type plots, while it was one of the intermediate treatment plots that contained live leaves for the longest period of time (see Figures S5 and S6 for separation by plot). The difference between the intermediate and control treatment is smaller than between either of them and the wet treatment. By the end of the experimental period all leaves were expected to have withered, regardless of treatment.

The statistical model did not converge for testing the interaction between treatment and week, even when grouping weeks or simplifying the structure of the model (i.e. using a glm instead of a mixed model). However, a week-by-week test showed that the proportions of live leaves in the wet treatment was significantly lower than the control in both the second (estimate=-0.30, SE=0.08, $p<0.001$) and third (estimate=-0.36, SE=0.08, $p<0.001$) week of measurements, as seen in the raw data means.
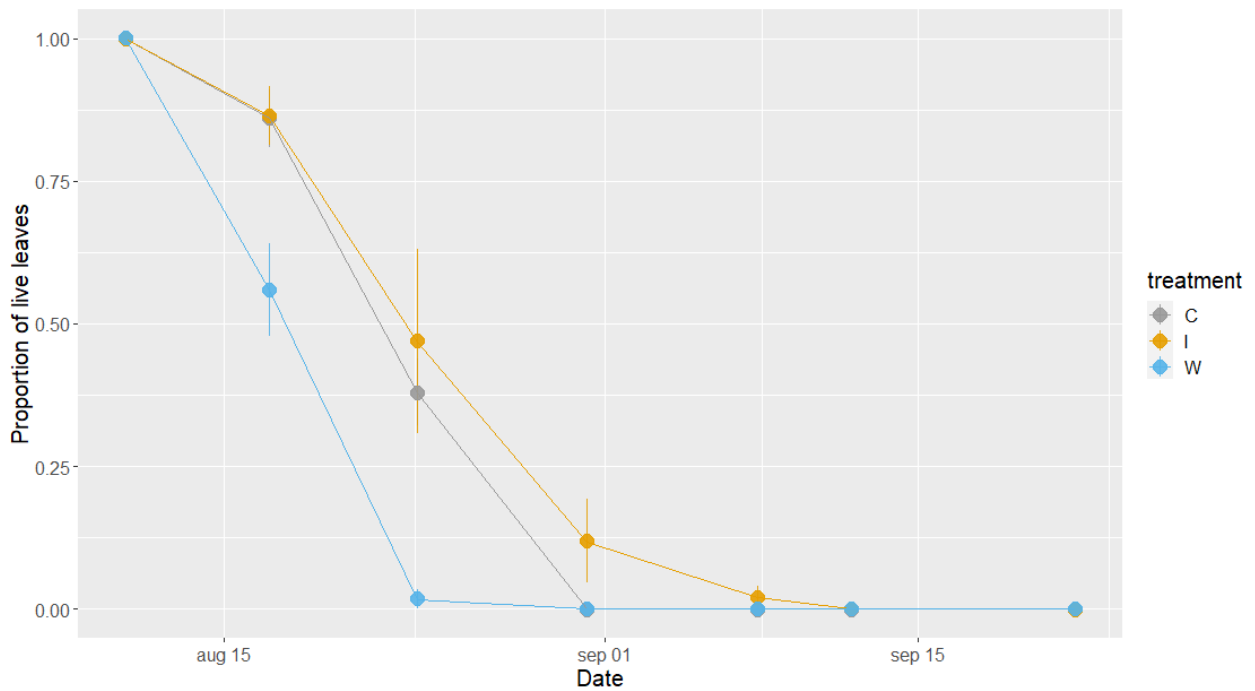
Figure 8: Raw data plot showing the mean proportion of live leaves of *Bistorta vivipara* in plots exposed to different watering treatments. Wet treatment (W) represented with blue lines, intermediate treatment (I) represented with orange lines, and control treatment (C) represented with gray lines.

4 Discussion

Climate change in the Arctic is expected to not only affect temperature but also hydrology, through increased precipitation and more rainfall at the expense of snowfall (Box et al., 2019). Several studies have linked water availability and soil moisture to plant species distribution and productivity, and noted it as an important factor in predicting changes to High Arctic ecosystems in the face of climate change (Bjorkman et al., 2018; Campbell et al., 2021; Gamon et al., 2013; Hodkinson et al., 1999). My study expands on this with insight into the connection between soil moisture and senescence at a species-specific level, with wider implications for a large Arctic herbivore. I tested the effects of increased soil moisture on the senescence of three of the most common plant species important to the Svalbard reindeer. Though all species responded positively to moderate increases in soil moisture, there were differences regarding tolerance for extreme moisture conditions. While the growing season for the grass *Alopecurus borealis* was significantly prolonged at both moderate and high levels of soil moisture, the forb *Bistorta vivipara* and the shrub *Salix polaris* responded positively only under a slight to moderate soil moisture increase and responded negatively to the highest levels of soil moisture. These findings suggest a prolonged growing season for all

three species under moderate increases in soil moisture but also indicate species differences in sensitivity to flooding events caused by heavy rainfall.

4.1 Effects of moderate increases in soil moisture

A. ovatus experienced a prolonged growing season with increasing moisture levels, with a greater proportion of leaves being green in late September in both the intermediate and wet treatment compared to the control. The rate of senescence for the intermediate treatment was relatively similar to that of the control, but still with a statistically significant improvement. *B. vivipara* and *S. polaris* also experienced slight positive reactions to the intermediate treatment compared to the control.

The timing of autumn senescence has previously been shown to correlate with moisture levels in July, where wetter conditions prolonged the senescence phase (Westergaard-Nielsen et al., 2017). Other studies have also shown a positive link between temperature and water, with plants benefitting from increased temperatures when water availability is simultaneously improved (Bjorkman et al., 2018; Winkler et al., 2016). Bjorkman et al. (2018) found that tall, resource-acquisitive plants in particular could benefit from a warmer and wetter climate, however Winkler et al. (2016) found that graminoids also experienced improved productivity from heating alone. A study from Greenland found that late season water limitation was the main reason for a faster rate of senescence, and a close relationship between soil moisture levels during the summer and the timing of the autumn season (Westergaard-Nielsen et al., 2017). Here, I have been one of the first to show the isolated effects of moisture levels on the senescence of high Arctic plants, with a positive effect on the graminoid *A. ovatus*, the shrub *S. polaris*, and the herb *B. vivipara* under moderate increases in soil moisture. This would indicate a positive effect on the growing season with a longer senescence period for these species, representing three different plant functional groups, under moderate increases in precipitation in the future.

4.2 Effects of high increases in soil moisture

The herb *B. vivipara* and the shrub *S. polaris* experienced strong negative reactions to the wet treatment with rapid senescence compared to the other treatments, despite having shown a positive response to the intermediate treatment. *A. ovatus*, on the other hand, responded in the opposite direction and the timing of senescence was significantly delayed with the wet treatment compared to the controls.

Livensperger et al. (2019) found that remotely sensed onset of senescence was affected by warming and snow-melt timing, with warmer and drier conditions leading to earlier senescence, but that effects on senescence rate was variable between years and species. Other studies have also shown species-specific responses to flooding in the Arctic. A study from Siberia investigating the effects of flooding on three *Salix* species found reduced photosynthetic activity in response to prolonged inundation (Fan et al., 2018), while a study from Iceland found a negative response to inundation on *Salix callicarpaea* x *lanata*, but little response from *Salix herbacea* (Thorhallsdottir, 1993). Thorhallsdottir (1993) also found that *B. vivipara* decreased in frequency in response to inundation. A study on tidal inundation on the Alaskan coast found that flooding reduced the biomass of *Salix ovalifolia* while the biomass of the graminoids *Poa arctica* and *Deschampsia caespitosa* increased (Person & Ruess, 2003). The authors believed that the graminoids were better than *S. ovalifolia* at exploiting changes in resources as experienced under increased salinity due to their higher growth rates. The results from these studies mostly align with my own, where *S. polaris* and *B. vivipara* responded negatively to extreme moisture levels and flooding through faster senescence, while the graminoid *A. ovatus* was able to delay its senescence. This highlights the importance of soil moisture levels on multiple factors of plant growth and senescence in the Arctic, and the need for species specific studies.

It is possible that *A. ovatus* was able to take better advantage of very high soil moisture than the other species due to physiological differences. The root system of a plant is the organ most sensitive to oxygen deprivation, and plants generally cannot sustain their growth under anoxic conditions for long (Armstrong et al., 1994). Most of the tissue mass of *A. ovatus* is found in the moss layer or above ground, however almost 25% can be found underground below the moss layer (Brooker & Van Der Wal, 2003). Additionally, it typically grows to a height between 7-25 cm tall (Svalbardflora, 2020a). *S. polaris* has its roots in the upper active layer of the permafrost (Owczarek, 2005), and more than 80% of its tissue mass is found in the moss layer with less than 4% found below that; *B. vivipara* grows even more shallow, with more than 90% of its tissue mass in the moss layer and less than 1% found below that (Brooker & Van Der Wal, 2003). When some of the plots in this study flooded, *A. ovatus* was therefore the species best suited to avoid complete submersion and anoxia as they could reach both deeper into the soil and further into the air than the other two species to facilitate gas exchange. This could explain why *A. ovatus* was the only species in my study to extend its

growing season in the wet treatment, and suggest that it could be a species more resistant to extreme weather events resulting from climate change.

Under flooding conditions, *S. polaris* and *B. vivipara* plants would experience submersion and anoxia, causing the rapid decline in live leaves. The plastic surrounding the intermediate and wet treatment plots would have prevented rainfall from draining through to deeper soil layers, and in the case of some of the wet plots the manually added water went beyond what the soil could absorb and effectively flooded the upper soil layer, suffocating the shallower roots. See S9 for pictures taken early and late in the season of one of the blocks that flooded, noting the browning of the wet treatment plot at the end of the study period compared to early season and the intermediate treatment. Myers-Smith et al. (2015) found that most of their study sites had a positive relationship between climate and growth in areas with high soil moisture, however eight sites showed a negative relationship. They explained this as a possible result of drought limitation, or that standing water, such as that experienced in some of the wet treatment plots in this study, could result in reduced growth and dieback.

Events of heavy rainfall are expected to increase in frequency on Svalbard, with a subsequent increase in flooding events particularly when such rainfall coincides with glacier melt in the summer (Hanssen-Bauer et al., 2019). This could have a strong negative impact on *S. polaris* and *B. vivipara* growing in flood prone areas. Under water-logged conditions other species such as mosses tend to dominate (Kemppinen et al., 2019), and so flood prone areas may in the future see a reduction in some herbs and graminoids and instead become more mossy.

4.3 Implications for the future and Svalbard reindeer

Though the effect was strongest for *A. ovatus*, all three species experienced delayed senescence from slight increases in soil moisture. This could indicate that a moderately wetter climate can lengthen the period of time with higher quality grazing for the reindeer, particularly in the areas that are not prone to flooding. This could also have a positive effect on the grazing of Svalbard reindeer, who favor the species used in this study (Bjørkvoll et al., 2009). Though graminoids typically make up the bulk of grazed plants both summer and winter, *S. polaris* makes up a higher proportion of the reindeers' diet both summer and winter compared to *A. ovatus*, while *B. vivipara* is favored during the summer (Bjørkvoll et al., 2009). Both negative and positive effects on the growth of these forbs, especially *S. polaris*, may therefore have consequences for the winter survival rate of the reindeer. The population of Svalbard reindeer have increased over the years, and winter starvation is the main cause of

death (Albon et al., 2017). An increase in the available plant biomass in the summer and autumn could be expected to improve winter survival rates especially in the face of icing from rain-on-snow events, as it would allow the animals to build up larger fat reserves by having access to high quality forage for a longer period of time (Albon et al., 2017; Loe et al., 2021; Tews et al., 2007).

Hydrological shifts in the landscape will affect which locations are more or less optimal for the growth of each species, leading to areas with increased and decreased biomass, respectively. This may in turn affect the distribution of reindeer, as they are selective grazers driven largely by quantity of live biomass (R. Van Der Wal et al., 2000). By reducing the moss layer, grazing by reindeer also facilitates the growth of the forbs and herbs they prefer to eat (R. Van Der Wal & Brooker, 2004), in a positive feedback loop between plant and herbivore. As a moss-dominated tundra helps to retain moisture and keep the soil cool, a shift towards a herbaceous state produces warmer soils and a deeper active layer (Ravolainen et al., 2020), which could strengthen this feedback loop with further consequences for plant communities on the tundra. On the other hand, in areas prone to flooding we may see a reduction in *B. vivipara* and *S. polaris*, and moss species may become more dominant (Kemppinen et al., 2019), possibly together with flood-tolerant grass such as *A. ovatus* and *P. arctica*. *P. arctica*, which was found to increase in biomass under flooding conditions even with increases in salinity (Person & Ruess, 2003), is also found on Svalbard and is commonly grazed on by reindeer (Bjørkvoll et al., 2009). The different responses of plants to changes in soil moisture as shown in my study indicate that climate change may have significant implications for plant senescence and distribution in the Arctic, with further implications for the population dynamics of Arctic herbivores.

5 Conclusion

The effects of climate change on high Arctic plants is dependent on multiple factors, where water availability in the soil plays a large part in determining plant growth and species composition. This study suggests that future increases in soil moisture levels may delay the senescence of some of the most important grazing species of the Svalbard reindeer, especially for graminoids such as *Alopecurus ovatus*. The two forbs *Salix polaris* and *Bistorta vivipara* can also be expected to respond positively to increases in soil moisture up to a certain point, after which their shallow roots may suffer from waterlogging and anoxia. Changes in water availability in the landscape may also cause shifts in plant communities and species

composition as conditions favor different species, which in return will change soil characteristics further. For the Svalbard reindeer, which are mostly regulated bottom-up based on food availability, such changes is likely to affect their distribution and ability to build up energy reserves before the winter. Understanding food availability in the autumn season is therefore of key importance, and here I have shown that water availability is a significant contributing factor to autumn senescence. Due to the heterogeneity of the effects of climate change in the Arctic, future studies should look into how moisture levels are predicted to change both at local scales and across different landscapes in order to understand how plant communities may change, as well as how this may affect the abundance and distribution of Arctic grazing species such as reindeer.

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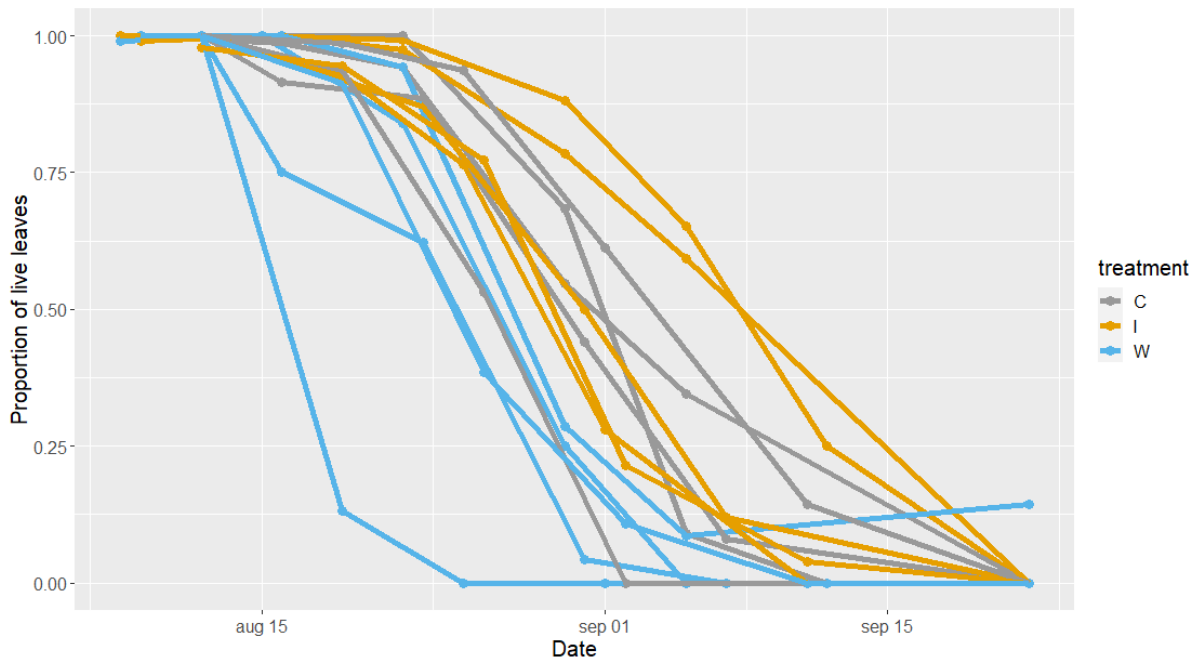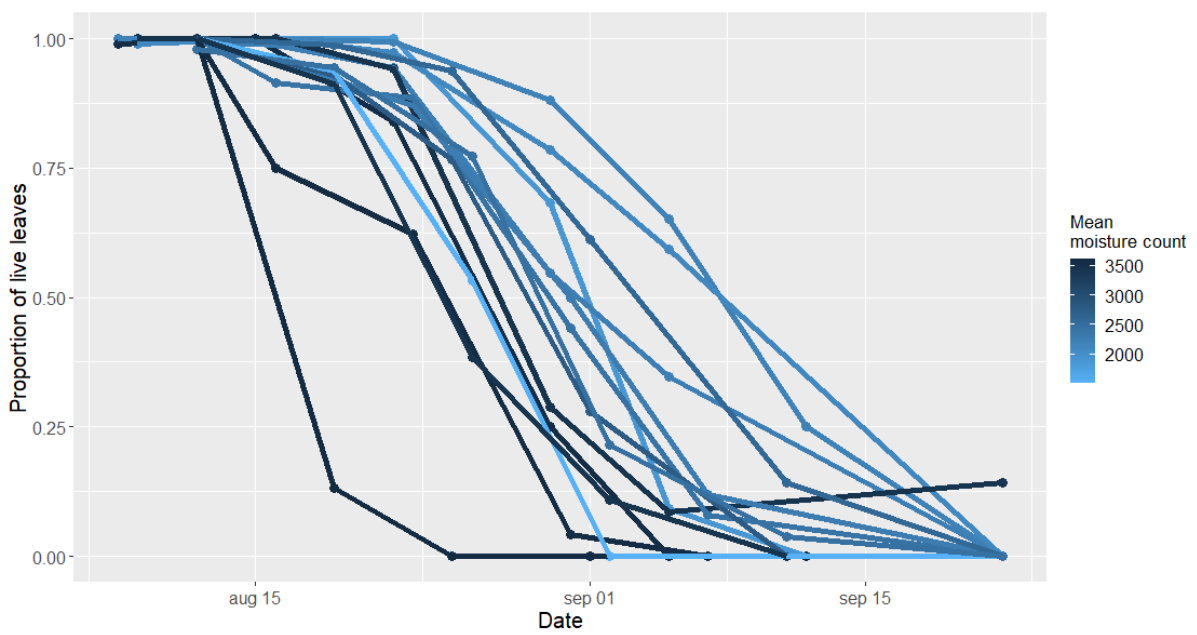
7 Appendices
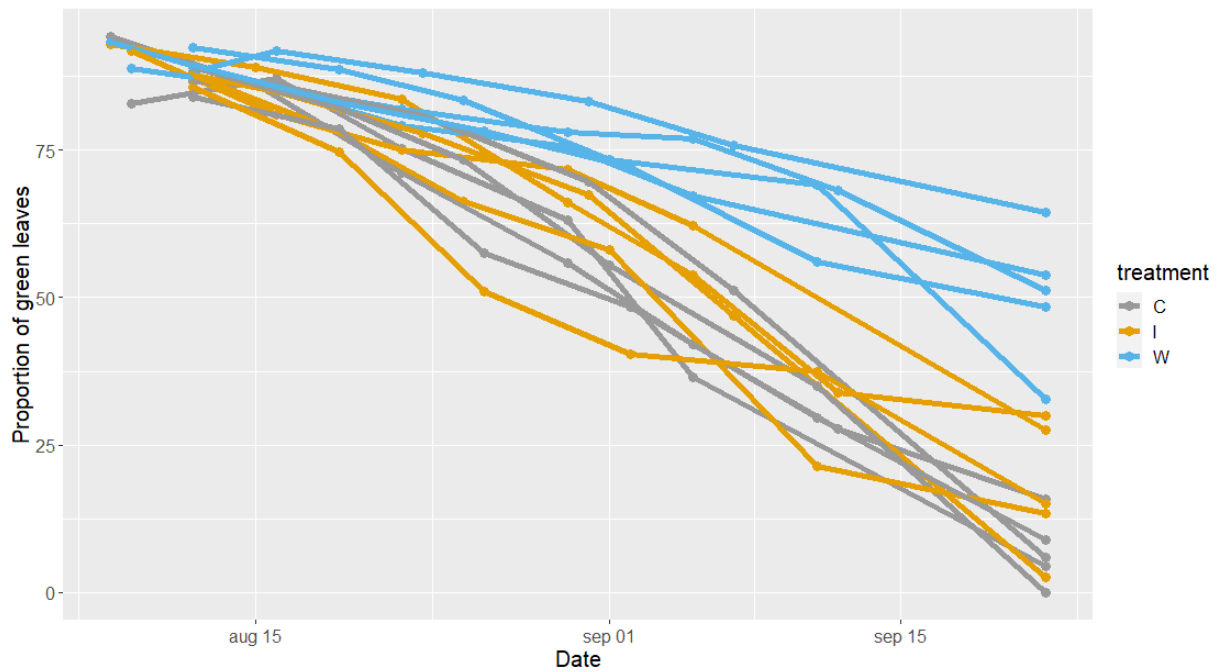
S1: Raw data showing the effects of treatment on *Alopecurus ovatus*. Each line represents a plot (n= 15). Wet treatment (W) represented with blue lines, intermediate treatment (I) represented with orange lines, and control treatment (C) represented with gray lines.
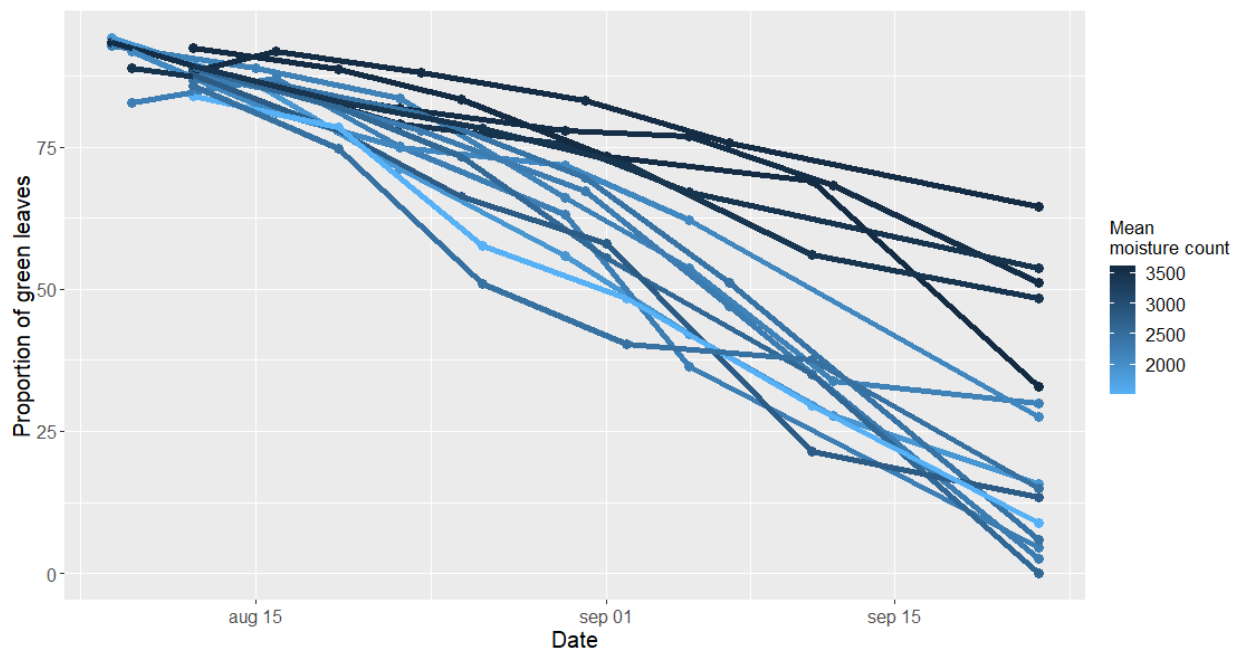
S2: Raw data showing the relationship between mean moisture count for each plot and the proportion of green leaves as autumn progresses for *Alopecurus ovatus*.

S3: Raw data showing the effects of treatment on *Salix polaris* in 2022. Each line represents a plot (n= 15). Wet treatment (W) represented with blue lines, intermediate treatment (I) represented with orange lines, and control treatment (C) represented with gray lines.

S4: Raw data showing the relationship between mean moisture count for each plot and the proportion of live leaves as autumn progresses for *Salix polaris*. Each line represents a plot (n= 15).
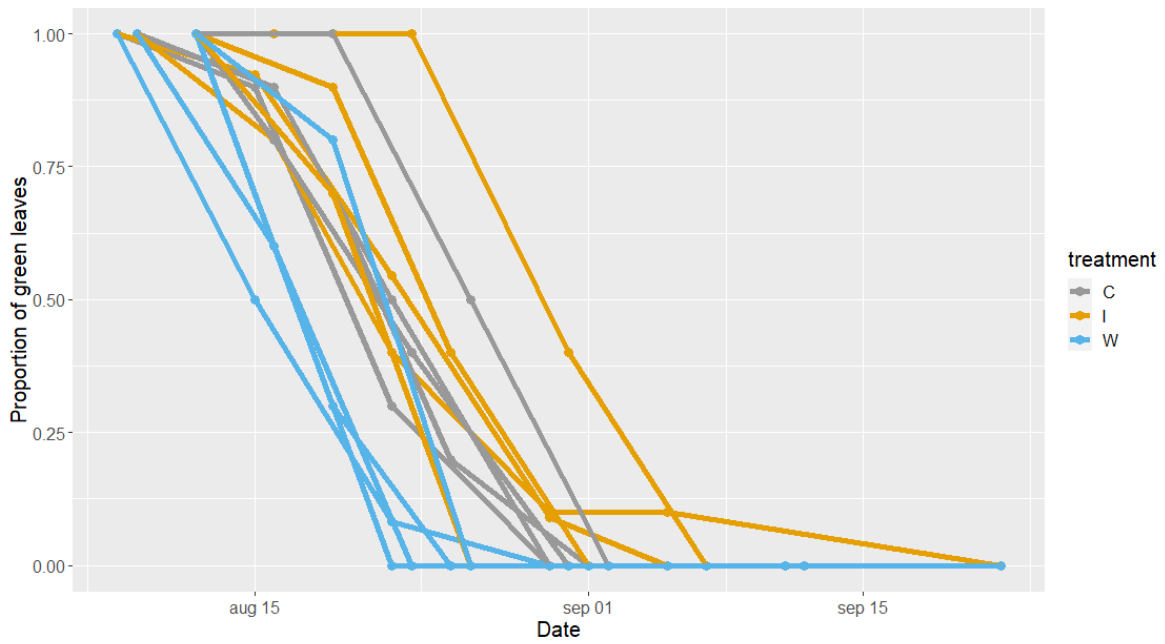
S5: Raw data showing the effects of treatment on *Bistorta vivipara* in 2022. Each line represents a plot (n= 15). Wet treatment (W) represented with blue lines, intermediate treatment (I) represented with orange lines, and control treatment (C) represented with gray lines.
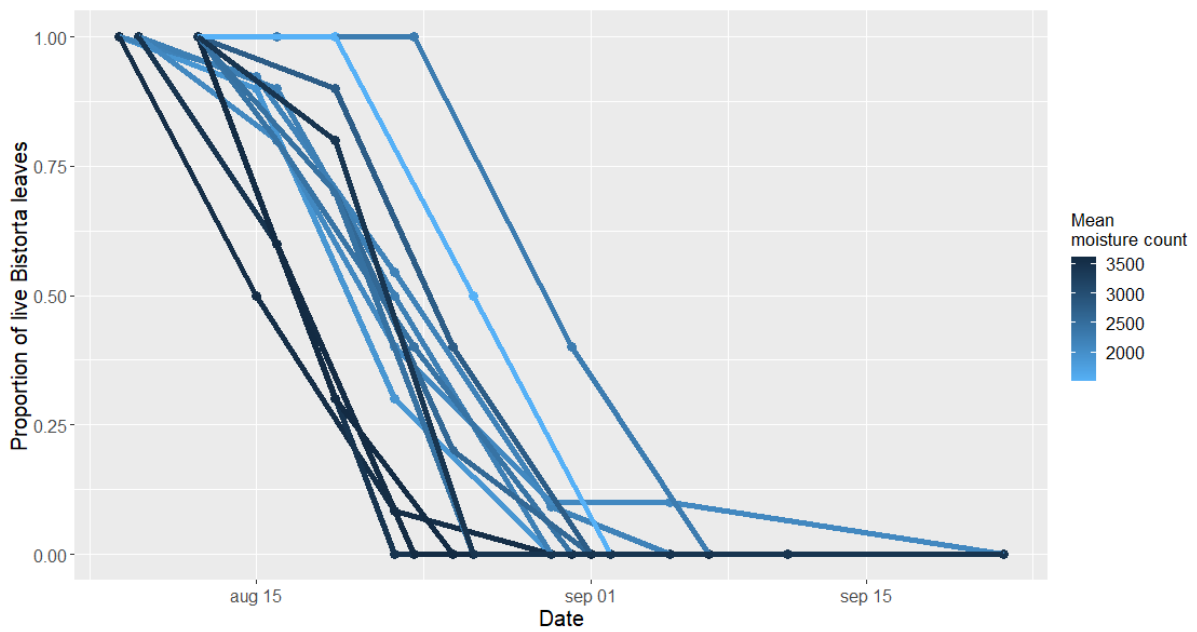
S6 : Raw data showing the relationship between mean moisture count for each plot and the proportion of live leaves as autumn progresses for *Bistorta vivipara*. Each line represents a plot (n= 15).

S7 : Photo of flooded wet treatment plot in block 4 (WW04), taken 19th August 2022.
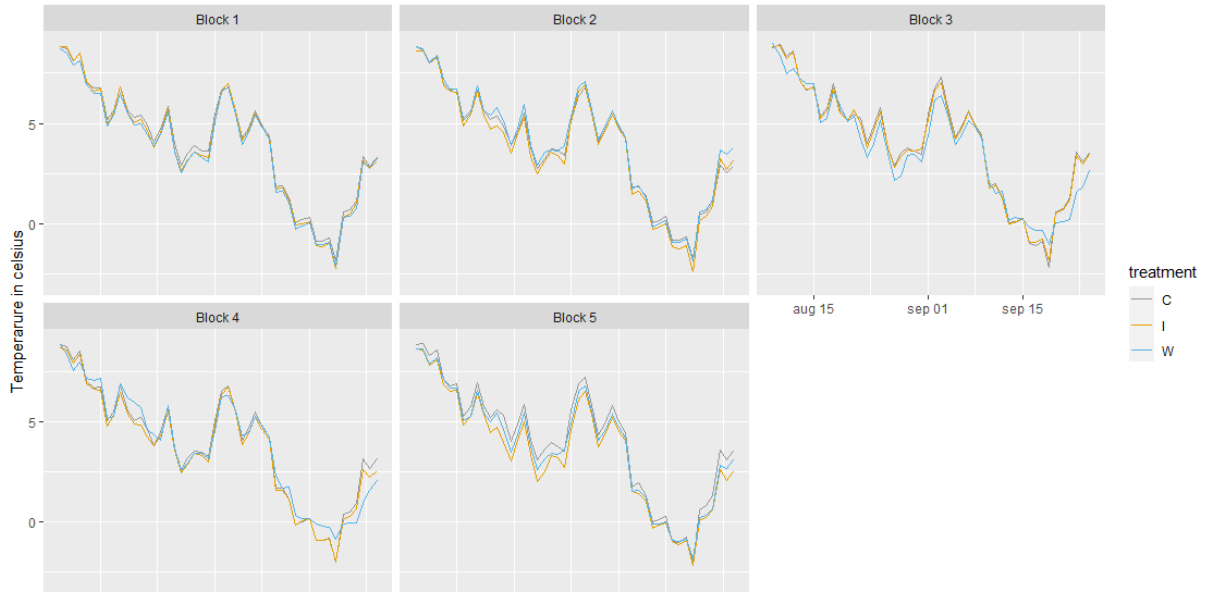
S8 : Photo of snow-covered plot taken 16th September 2022.

S9 : Photo of block 1 taken early (left side, 12th August 2022) and late (right side, 5th September 2022) in the study period. Wet treatment shown in the top two photos and intermediate treatment shown in the bottom two photos.

Average daily temperature at ground level

S10: Average daily temperature measurements at ground level. Wet treatment (W) represented with blue lines, intermediate treatment (I) represented with orange lines, and control treatment (C) represented with gray lines.

Average daily air temperature
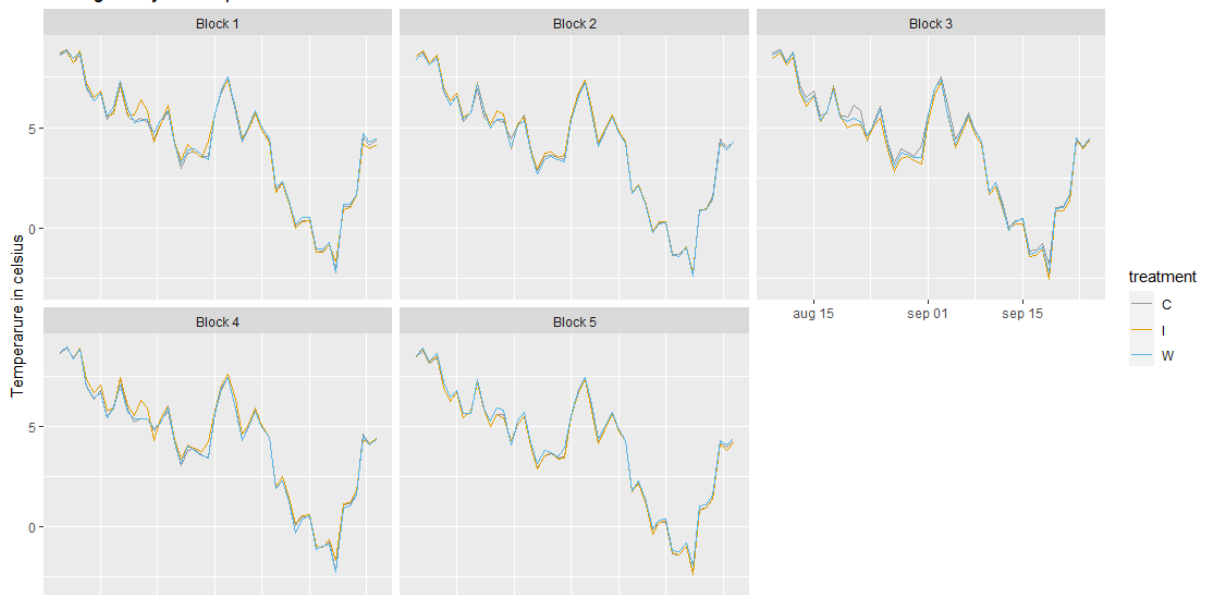
S11: Average daily air temperature measurements, measured at ca. 15 cm above ground level. Wet treatment (W) represented with blue lines, intermediate treatment (I) represented with orange lines, and control treatment (C) represented with gray lines.