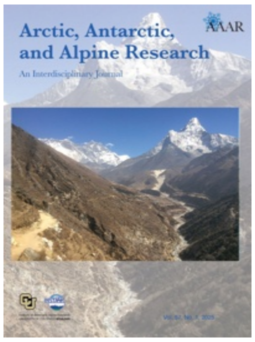

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Waterlogging of soil induces diverging rates of senescence in Svalbard reindeer forage plants

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ABSTRACT

As climate change is unfolding faster in the Arctic than in any other biome, thermal and hydrological changes are predicted to reshape Arctic ecosystems. Water availability is expected to affect the end of the plant growth season, a time period essential for accretion of fat stores in Arctic herbivores, influencing their survival. We experimentally tested how different levels of soil moisture influenced timing and rate of senescence of a grass (*Alopecurus ovatus*), forb (*Bistorta vivipara*) and dwarf shrub (*Salix polaris*), important forage plants for a keystone herbivore, Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Moderately increased soil moisture slightly delayed the timing of senescence in the forb and shrub. However, waterlogging reduced the growing season of the forb and shrub but considerably extended that of the grass. In "saturated" (waterlogged) plots, 40 percent of initial grass biomass remained green until the end of the experiment (onset of snow and frost), compared to <10 percent in "elevated soil moisture" and "control" plots. These results indicate that soil moisture moderates rates of plant senescence, with some species benefiting from saturated soils. Waterlogging soils may extend the time period over which flood-resilient grasses senesce, to the nutritional benefit of Arctic herbivores such as Svalbard reindeer.

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Arctic herbivores; climate change; field experiment; forage plants; Svalbard reindeer; soil moisture manipulation; waterlogging

Introduction

The Arctic is experiencing climate change faster than the rest of the Northern Hemisphere, with rising temperatures and increasing moisture being key contributors (Box et al. 2019). As a consequence, the growing season for plants is lengthening, with earlier onset of spring and later end of autumn (Park et al. 2016). This accentuates the "greening" observed in many parts of the Arctic (Bhatt et al. 2010; Elmendorf et al. 2012; Van der Wal and Stien 2014; Myers-Smith et al. 2020), the magnitude of which can be mediated by hydrological characteristics (Campbell et al. 2020). Although increased temperature plays a main role in plant growth and onset of senescence (Gehrmann, Ziegler, and Cooper 2022; Möhl, von Büren, and Hiltbrunner 2022), its effect on rate of senescence is variable, with soil moisture as an important and understudied contributing factor (Livensperger et al. 2019). How changes in soil moisture affect both timing and rate of senescence in key Arctic plant groups is important knowledge to predict future growing season lengths across the Arctic tundra, with implications for the plane of nutrition of its herbivores.

Because Arctic plants have such a short growing season, the timing of autumn senescence is of particular importance not only to maximize plant growth and seed production but also to ensure effective nutrient resorption and development of frost hardiness (Gehrmann, Ziegler, and Cooper 2022). For large herbivores, onset of senescence marks the point where feeding conditions deteriorate. If plants senesce later, large herbivores have extended access to nutrients that are critical for accretion of energy stores prior to the food-limited season of winter (Gallinat, Primack, and Wagner et al. 2015; Hurley et al. 2014). Whereas some studies have found that higher temperatures delay senescence (Marchand et al. 2004; May et al. 2017; Collins et al. 2021), others have found the opposite, possibly due to high temperatures causing water limitation (Oberbauer et al. 2013; Livensperger et al. 2019; Gehrmann, Ziegler, and Cooper

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2022). Similarly, the limited number of studies focused on factors influencing rate of senescence have also found mixed responses among plant species and community types to warming (May et al. 2017; Livensperger et al. 2019). How water availability structures plant communities and affects plant growth is species specific and dependent on water quantity and time of year (Kemppinen et al. 2019). Despite soil moisture being an important factor in determining climate sensitivity of plant growth and senescence in the Arctic (Myers-Smith et al., 2015; Livensperger et al. 2019), few studies have tested the isolated effects of different soil moisture levels, including differences between plant functional groups and species.

Along with the rest of the Arctic, the archipelago of Svalbard is experiencing increasing temperatures and hydrological changes (Sokolíčková et al. 2022). Svalbard is expected to face considerably higher temperatures, more precipitation, shorter snow seasons, more frequent extreme weather events, increased glacial melt-off and disappearing permafrost (Hanssen-Bauer et al. 2019). There is evidence of a strong positive effect of summer temperatures on the aboveground biomass of multiple vascular plants in Svalbard (Van der Wal and Stien 2014) as well as their (delayed) senescence (Collins et al. 2021). The plant growing season in Svalbard ranges from one to three months depending on bioclimatic zone (Jónsdóttir 2005). Though the number of days with average temperature above 5°C ("growing days") on Svalbard is predicted to double by 2100, the amount of rainfall and potential flooding events are predicted to increase, too, especially in autumn (Hanssen-Bauer et al. 2019). Moreover, active layer depth is rapidly increasing as permafrost is thawing, notably due to consecutive years of winter warming (Schuh, Frampton, and Christiansen 2017). An increase in water flux can create possibilities for new water flow paths and retention, all with a profound effect on surface hydrology and downstream environments (Nowak et al. 2021). Such changes in hydrology can have a large impact on Svalbard's plant communities and their spatial configuration, because species have different optimal growing conditions related to soil moisture (Hodkinson et al. 1999).

The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) is the only large herbivore in Svalbard, and this subspecies is still recovering from a situation of extreme overharvesting (Le Moullec, Pederson et al. 2019b). Svalbard reindeer have much lower access to lichens in autumn and winter than other *Rangifer* subspecies (Van der Wal 2006). The near-absence of lichens from their diets (Bjørkvoll et al. 2009) means that climate change–related effects on vascular plants are consequently a major determinant of future population growth of this endemic subspecies. We investigated the effects of increased soil moisture on the timing and rate of senescence of three of the most common vascular plant species favoured by Svalbard reindeer (Bjørkvoll et al. 2009): the grass *Alopecurus ovatus*, the forb *Bistorta vivipara* and the dwarf shrub *Salix polaris*. By altering soil moisture conditions of these plants in a replicated field experiment, we tested whether elevated and saturated levels of soil moisture influence leaf senescence. Because autumn conditions are known to have carryover effects on Svalbard reindeer body condition and calving rates in spring (Albon et al. 2017; Loe et al. 2021), we discuss our findings in light of relaxed food limitation for herbivores in a warming Arctic.

Materials and methods

Study area

We conducted fieldwork from the 25th of July to the 22nd of September 2022 in Adventdalen, high-Arctic Svalbard (Figure S1; 78.20° N, 15.81° E). The valley belongs to the phytogeographical zone "middle Arctic tundra" (Jónsdóttir 2005), with moss–graminoid vegetation (Ravolainen et al. 2020) being well-represented and parts thereof strongly affected by flooding (Johansen, Tømmervik, and Karlsen 2009; Norsk Polarinstituttt 2022). The decadal (2011–2021) mean July to September air temperature for the area was 5.8°C and precipitation was 74.5 mm per year. In 2022, the year of study, mean July to September air temperature was 6.5°C and precipitation was close to the decadal mean, at 73.3 mm (Meteorologisk institutt 2023). Notably, rainfall in August contributed to more than half of the growing season precipitation (41.5 mm), with 31.3 mm falling over three days (18–20 August). The amount of precipitation in August 2022 was 52 percent higher than the August decadal average of 27.3 mm (Meteorologisk institutt 2023).

The study area is underlain by permafrost, which, in combination with surface topography and glacial melt, strongly influences the hydrology because the active layer is shallow (1–2 m; Hanssen-Bauer et al. 2019). This interaction gives rise to small-scale spatial heterogeneity of hydrological conditions and a mosaic of dry, mesic and wet tundra (Sjögersten, Woodin, and Van der Wal 2006). Our experimental site in mesic tundra had "silty clay loam" soils (following Thien 1979; see Figure S2 for a representative photo) across a moisture gradient from dry heath to wet marsh (akin to those studied by Scymánski et al. [2022], less than 1 km away). Our site is comparable to a nearby mesic tundra site that Sjögersten, Woodin and Van der Wal (2006) reported is frequently water saturated late in the growing season.

Study species

The three focal species, *Alopecurus ovatus, Bistorta vivipara* and *Salix polaris*, represent different plant functional groups. Although their soil moisture optima may differ, all three species are common among an array of habitats and co-occur in mesic tundra. We focus on this vegetation type because it is a key feeding habitat of reindeer and has high potential for altered hydrology due to its position in the landscape. Species names follow the annotated checklist of the Panarctic Flora (http://panarcticflora.org/). *Alopecurus ovatus* (hereafter *Alopecurus*) is a perennial, moisture-dependent grass found in moist meadows, shallow mires, sediment plains and moss tundra and is common throughout Svalbard. Aerial shoots grow from branched, interconnected rhizomes. The relatively long leaves (typically 5–10 cm) and culm (typically 7–25 cm) make it one of the taller grasses (Elven et al. 2020) and hence an attractive food item for reindeer. *Salix polaris* (hereafter *Salix*) is a small perennial shrub of arctic–alpine environments and one of the most common plants in Svalbard. It forms extensive mats with its branched stems and is particularly dominant in drier habitats, such as heaths and ridges (Van der Wal and Stien 2014). The belowground structure of *Salix* generally consist of a core root with several thinner lateral roots, but in moist habitats much more complex or fine-rooted individuals seem to dominate (Le Moullec, Buchwal et al. 2019a). Shoots are typically 1 to 3 cm in height, bearing leaves ca. 1.5 cm long and wide (Elven et al. 2020). *Salix* leaves are extensively fed upon by reindeer, including through stripping them off shoots (R.vdW. and S.P.H.D., pers. obs.). *Bistorta vivipara* (hereafter *Bistorta*) is a perennial forb of upper montane to alpine mesic meadows and stream sides, or occasionally more xeric alpine sites on shallow soil (Marr et al. 2013), and is common throughout Svalbard. Plants grow as separate units, with one or several stems emerging from a single tuberous rhizome and leaves of ca. 2 to 5 cm long (Elven et al. 2020). Leaf forage quality of this species is particularly high (second lowest C-to-N-ratio of twenty-seven plants sampled during late summer in the wider study area; data from Van der Wal and Hessen 2009).

Experimental study design and data collection

To investigate the effects of increased soil moisture on the timing of senescence, we used a randomized block design where five blocks of mesic tundra with homogenous vegetation were identified and established between the 25th and the 27th of July 2022. Each block contained three 40 cm × 40 cm plots within 1 to 3 m of each other. We cut the perimeter of each plot with a bread knife to a depth of about 15 cm into the ground, after which we lifted the turf out of the ground and subjected it to one of three different treatments described below (Figure S3). Mean moss and organic layer depth were 4 mm (SE = 0.7) and 45 mm (SE = 5.6), respectively.

Treatments

We manipulated wetness of the soil to generate three conditions—“control,” “elevated” and “saturated” soil moisture levels—simulating under field conditions hydrological state changes towards wetter and waterlogged conditions as can occur through a variety of mechanisms in notably lower-lying tundra due to a warmer and wetter high-Arctic climate (Nowak et al. 2021). We will use those terms for the treatments throughout the article. The first type of treatment, control, reflects current natural levels of soil moisture, whereby the turf was dug out, lifted up and placed back into the ground. For the two other types of treatment, we positioned a waterproof plastic sheet into the hole, large enough to cover both the bottom and all four sides, before placing the turf back. The purpose of the plastic layer between the plots and the ground was to prevent water from the surrounding area from entering the plots, making it easier to control soil moisture. The second treatment, elevated soil moisture, reflected conditions that wet the soil more and keep it wet for longer. We achieved this through restricting drainage by means of the above-described plastic sheet while trapping all rainfall on the turf. No other water was added. The third treatment, saturated, mimicked a hydrological regime that maintains soils in a water-saturated state (i.e. waterlogged throughout summer (Figure S4). The amount of water needed to keep these plots saturated varied through the experiment. Two litres were added on both 25th and 27th July; then 4 L on each of the 29th of July and the 2nd and 5th of August; and a final 1 L on 12th of August.

To establish how the different treatments influenced soil moisture throughout the field experiment, we placed TOMST TMS-4 data loggers in each plot, which were set at a recording frequency of every 15 minutes. Soil moisture was recorded using the time domain transmission method, measuring across approximately 14cm depth. Although extending deeper than the organic layer of decaying moss (Figure S2), a substantial proportion of live biomass (roots) is found deeper down in the soil (Bardgett et al. 2007), suggesting that our soil moisture measures are a sufficiently good index for the moisture conditions experienced by the plants under study. We converted time domain transmission to volumetric soil moisture (the ratio of the volume of water to the unit volume of soil) using the R package myClim (Wild et al. 2019) and the function "mc_calc_vwc" set to soil type "silt loam," which corresponds to field validation of the soil type. Mean daily moisture levels during the study period were significantly different between saturated and both elevated and control treatments ($p < 0.001$). Over the entire study period, there was no significant difference between elevated and control treatments ($p = 0.42$; Table S1), but moisture levels in elevated plots clearly exceeded control levels after rainfall events, as intended (Figure 1a).

Several bouts of heavy rainfall that occurred during our experiment also raised soil moisture in our control plots and with prolonged water retention (Figure 1a). We did no tests to determine how freely draining our silty clay loam soils were, but, based on field observation and literature (e.g. Sohlberg and Bliss 1984; Nowak et al. 2021), we expect that the apparent ability to retain

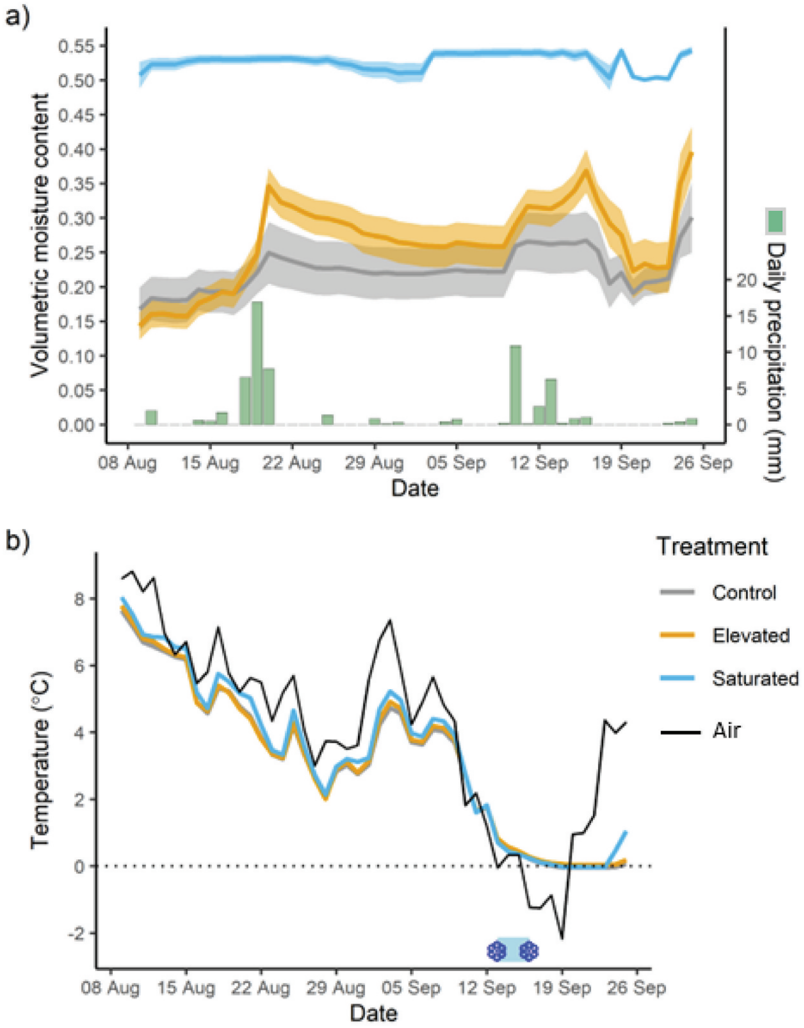

Figure 1. Mean daily (a) soil moisture content and (b) soil temperature across the five blocks for each of the treatments, "saturated" (blue), "elevated" (yellow) and "control" (grey line). In (a) green bars show daily precipitation in millimetres per day (secondary *y*-axis), and error bands around the treatment lines are 95 percent confidence intervals. In (b) the horizontal dotted line represents zero degrees and the blue bar with snowflake symbols shows days with snowfall; mean daily air temperature measured 15 cm aboveground is also depicted (as black line).

moisture from rainfall for several weeks was due to a combination of the soils not being freely draining, surface topography and possibly additional lateral flow through the active layer. By catching rainfall more effectively, the plastic surrounding the elevated soil moisture plots allowed for soil moisture to quickly rise to a higher level, but the rate at which soil moisture declined in the days and weeks thereafter was actually greater than that in the controls. Although the plastic should have prevented lateral flow, it also prevented captured rainfall from draining into deeper soil layers. Thus, the observed soil moisture decay curve does not necessarily demonstrate how freely draining the soil is in this site. For the elevated treatment plots, regardless of the mechanism behind increased soil moisture, we did obtain moisture levels that were periodically greater than that of the control, which was the goal of the treatment.

Loggers also measured temperature at approximately +15, 0 and −6 cm relative to the moss–soil interface. One cold spell during the latter part of the experiment brought air temperatures down to −2°C (Figure 1b). The lowest soil temperature measured during the cold spell was −0.18°C. To check the possibility that our moisture treatments affected freezing of the soil differentially, we fitted a linear mixed model with probability of subzero soil temperature as a binomial response, treatment as a predictor and plot ID within block as a nested random intercept. This revealed that the probability of subzero soil temperatures did not differ among treatments ($p = 0.31$).

Senescence data were collected weekly between the 7th of August and the 22th of September 2022 (seven weeks); methods varied slightly for each of the three focal species to accommodate for differences in morphology. In week 6, between the 12th and 18th of September, snowfall and resulting snow cover meant that we were only able to record measurements in one of the five blocks (Figure S5).

Alopecurus ovatus

In each plot, we marked ten *Alopecurus* shoots. Each shoot was marked with a thin strand of coloured yarn tied around its base, so they could be readily re-identified. For each individually marked shoot, we recorded the number of leaves and the percentage of greenness for each of them. Additionally, the length of each leaf was determined with callipers during the first measurement to provide initial biomass estimates.

Salix polaris

Due to the large number of *Salix* leaves, we marked out a single 10 cm × 10 cm square with toothpicks at the corners, to count the number of *Salix* leaves of different colour (green, yellow, red or brown) within each (40 cm × 40 cm) plot. We placed these measuring areas far enough away from the edges of turves to prevent influence from possible cutting-induced senescence. Upon recording, a thin wooden frame was slotted over the four toothpicks and measurements were taken from the same plot every time. Leaves were included in counts as long as they remained attached to the plant.

Bistorta vivipara

We selected and marked, with a toothpick, ten individual *Bistorta* "shoots" per plot and determined the number of leaves attached to each plant as well as their predominant colour (green, yellow, red or brown).

In total, we obtained senescence data for all leaves on 150 *Alopecurus* shoots throughout the duration of the field experiment. For *Bistorta*, we started with 168 leaves but lost some over time (final count was 153 leaves). Due to the large number of *Salix* leaves, we did not follow them at an individual level; instead, we counted all leaves attached to plants within the measuring area during each measurement round (range of counts per recording, 0–293). Leaves were considered alive if they were recorded as green for *Alopecurus* and green, yellow or red for *Salix* and *Bistorta*.

Statistical analysis

We conducted all statistical analyses in RStudio v1.4.1717. Leaf senescence rates were statistically analysed for all three species. Given the importance of grasses as food source of Svalbard reindeer during autumn, we gathered more detailed data for *Alopecurus* than for the other two species. This included measurements that allowed us to estimate loss of green biomass over time.

Estimating biomass loss of *Alopecurus*

We estimated whole ramet survival using the function "surv" of the package "survival" (Therneau 2023), and predicted and plotted treatment-specific Kaplan-Meyer survival curves using the functions "survfit" and "ggsurvplot" of the package "survminer" (Kassambara, Kosinski and Biecek 2021). A log-rank test was used to assess overall difference in survival among treatments. Green biomass of *Alopecurus* was "lost" over time through three hierarchical processes: (a) the death of whole ramets (i.e. individual "shoots"); (b) full senescence or disappearance of leaves on still live ramets; and (c) decreasing green proportion of leaves still alive. Length of all leaves per marked ramet (ranging from one to five) was measured only at the start of the experiment, while number of remaining leaves per ramet and percentage green of each leaf were recorded throughout the experiment. We assumed that ramets were fully grown at the start of the experiment and thus that initial length was representative for leaf length throughout the experiment. For each ramet and measurement round, we summed the initial lengths of remaining leaves and converted this to biomass. Conversion to biomass was made using the relationship between leaf length (mm) and their dry mass (mg; $\beta = 0.165$, $r^2 = 0.9$, $p < 0.001$; dried at 70°C). Remaining total ramet biomass was multiplied with the proportion green of the leaf (or mean proportion in cases with more than one leaf) to arrive at green biomass per ramet. For each measurement round, we summed the amount of green biomass remaining in each treatment and block and divided this sum by the initial biomass. This fixates the initial green biomass value at 1 but allows variable decay rates for each of the five replicates per treatment and block.

Statistical tests of treatment effects on senescence rates

Generalized linear mixed models were used to model how green proportion of leaves (*Alopecurus*; process c above) and count of live leaves (*Salix* and *Bistorta*) changed by measurement date, treatment and their interaction. To select the most parsimonious model, we conducted backward model selection in the form of likelihood ratio tests (LRT; using the "anova" function), starting from the full model. If the interaction was retained in the best model, this was statistical support for treatment effects on senescence rates. Model specification differed slightly across species. For *Alopecurus*, model errors were assumed to follow a binomial distribution, and plant ID was nested within block as a random intercept. To allow for as simple a model as possible, measurement date was fitted as continuous variable, because preliminary plotting showed no strong deviation from linearity. *Salix* and *Bistorta* models were fitted with a Poisson error distribution; block was fitted as a random intercept, and the number of live leaves per plot at first measuring date was used as an offset variable to account for different starting values. Measurement date was fitted as a categorical variable for both *Bistorta* and *Salix*, because of strong deviation from linear trends over time. For *Bistorta*, the generalized linear mixed model did not converge. We therefore used a generalized linear model to test for differences in the number of live leaves for weekly measurement rounds where large visual differences between treatments were observed in the raw data.

Results

Alopecurus

The type of treatment strongly influenced the speed at which ramets (i.e. units composed of a stem with multiple leaves) lost all signs of green ($\chi^2 = 32.1$, df = 2, $p < 0.001$). This process started more than two weeks earlier in *Alopecurus* in control and elevated soil moisture treatments compared to those in the water-saturated treatment (Figure 2a). Senescence at the level of ramets in the two drier treatments made a step change when autumn frost hit the system for the first time, just after mid-September, but in the wettest treatment this effect was barely noticeable. By the end of the experiment (22nd of September), 88 percent of ramets had fully senesced in control plots, 68 percent in elevated soil moisture plots and 38 percent in saturated plots. The mean number of green leaves on surviving ramets (Figure 2b) and the average proportion of green of those leaves (Figure 2c) declined in a much more gradual, continuous way. Again, this process was influenced by our treatments (LRT: $p < 0.001$; Table 1). Compared to in the controls, leaf senescence was slightly slower in *Alopecurus* subjected to elevated soil moisture ($p = 0.046$) but much slower when in saturated soils ($p < 0.001$; Figure 2c). By the end of the experimental period, 37 percent of the initial green biomass of *Alopecurus* remained in the saturated treatment; corresponding figures for elevated and control treatments were 6 and 2 percent, respectively (Figure 2d).

Salix

Soil moisture treatment also affected senescence rate in *Salix*, measured as number of live leaves over time (LRT: $p < 0.001$; Table 2). Unlike for *Alopecurus*, the saturated treatment promoted senescence in *Salix* (Figure S6). Plants in the saturated plots showed advanced senescence right from the start in mid-August, with half of its live leaves lost a week earlier than in the control and elevated soil moisture plots (Figure 3). For a brief period in the end of August, the proportion of live leaves was marginally higher in elevated soil moisture compared to control plots. By mid to late September, almost all plants had withered regardless of treatment (Figure 3).

Bistorta

Bistorta in saturated soils senesced even more rapidly than *Salix* and all leaves were gone after two weeks of treatment, in late August (Figure 4). The statistical model testing for treatment effect on senescence rate did not converge. However, a week-by-week test showed that proportions of live leaves in the saturated plots were significantly lower than in the control plots for both the second (22th of August: estimate = −0.30, SE = 0.08, $p < .001$) and third (29th of August: estimate = −0.36, SE = 0.08, $p < 0.001$) weeks of measurement. There was a slightly greater proportion of live leaves at the end of August in elevated soil moisture

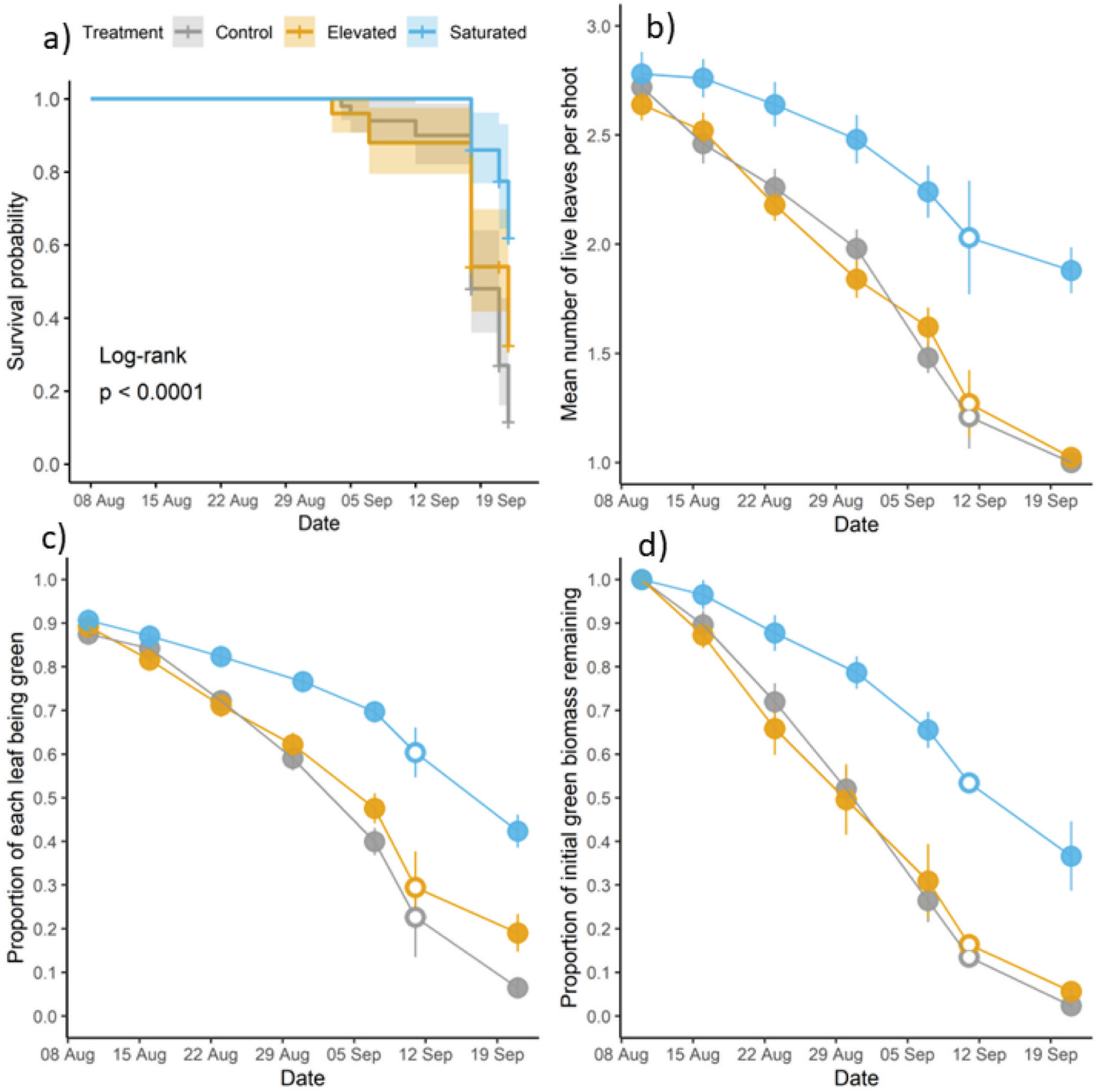

Figure 2. Effect of experimental soil moisture treatments on *Alopecurus ovatus* senescence during August and September regarding (a) survival of individual shoots, (b) number of remaining live leaves per shoot, and (c) proportion of each leaf remaining green. Points are raw data means and error bars are ±1 SE. Together, (a)–(c) were used to (d) estimate the proportion of initial green biomass remaining after accounting for processes (a)–(c). The "saturated" treatment is represented by blue lines, "elevated" treatment by orange lines and "control" treatment by grey lines. The open circles in (b) and (c) represent the week where measurements could only be recorded for one block, with data extrapolated from other weeks to calculate an approximate mean.

Table 1. Estimates of a logistic mixed effects model for *Alopecurus ovatus,* summarizing the effects of soil moisture treatments on the proportion of leaves that are green throughout the season (August–September).

	Estimate	SE	*z*	*p*
Intercept	0.671	0.171	3.93	<0.001
Treatment E vs. C	0.225	0.151	1.49	0.136
Treatment S vs. C	0.960	0.154	6.24	<0.001
Date (scaled)	−1.701	0.144	−11.84	<0.001
Treatment (E vs. C) × Date	0.371	0.186	2.00	0.046
Treatment (S vs. C) × Date	0.911	0.171	5.32	<0.001

Treatments were "control" (C), "elevated" soil moisture (E) and "saturated" (waterlogged) (S). Date was fitted as continuous variable in the model. Block (SD = 0.53) and individual within block (SD = 0.002) were included as nested random effects to account for the study design.

Table 2. Estimates of a Poisson generalized linear mixed effects model for *Salix polaris*, summarizing the effects of our soil moisture manipulations on the number of live leaves throughout the season (August–September).

	Estimate	SE	*z*	*p*
Intercept	−0.03	0.08	−0.41	0.685
Treatment E vs. C	0.01	0.05	0.14	0.890
Treatment S vs. C	−0.03	0.05	−0.68	0.494
Date 15 August (vs. 8 August)	−0.25	0.05	−4.72	<0.001
Date 22 August (vs. 8 August)	−0.51	0.06	−8.82	<0.001
Date 29 August (vs. 8 August)	−1.23	0.07	−16.61	<0.001
Date 5–19 Sep (vs. 8 August)	−4.17	0.20	−21.30	<0.001
Treatment E: Date 15 August (vs. 8 August)	0.07	0.08	1.00	0.319
Treatment S: Date 15 August (vs. 8 August)	−0.19	0.08	−2.48	0.013
Treatment E: Date 22 August (vs. 8 August)	0.04	0.08	0.48	0.634
Treatment S: Date 22 August (vs. 8 August)	−0.60	0.09	−6.77	<0.001
Treatment E: Date 29 August (vs. 8 August)	0.25	0.10	2.48	0.013
Treatment S: Date 29 August (vs. 8 August)	−1.75	0.17	−10.28	<0.001
Treatment E: Date 5–19 September (vs. 8 August)	0.98	0.23	4.24	<0.001
Treatment S: Date 5–19 September (vs. 8 August)	−1.82	0.54	−3.38	0.001

Treatments were "control" (C), "elevated" soil moisture (E) and "saturated" (S). Date was treated as a categorical variable in the model because the senescence pattern over time was not linear. Measurement dates in September had to be combined into one class for the model to converge. Reference levels are "control" for treatment effects and first date of the experiment (8th of August 2022) for effects over time. Block was included as a random intercept (SD = 0.17).

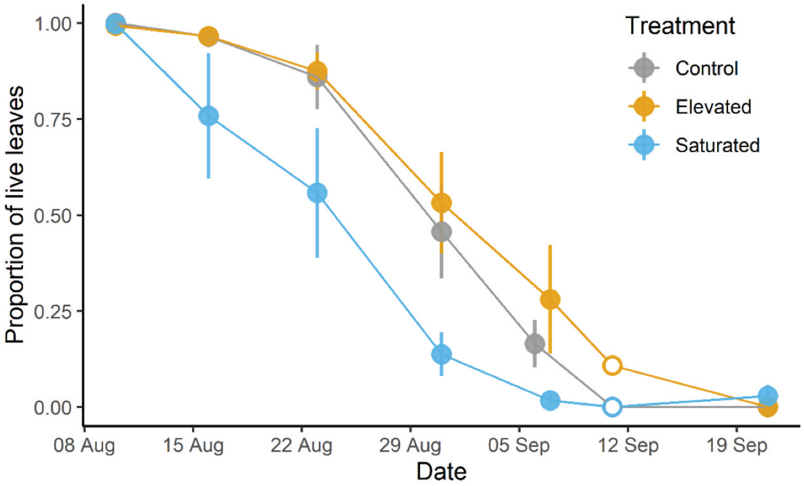

Figure 3. Effects of experimental soil moisture treatments on the mean proportion of live leaves of *Salix polaris* during August and September ("saturated" in blue, "elevated" in orange, "control" in grey). Points are raw data means and error bars are ±1 SE. The open circles represent the week where measurements could only be recorded for one block, with data extrapolated from other weeks to calculate an approximate mean.

compared to control plots (Figure 4), amounting to a week's difference in senescence of the last remaining leaves. By early September, all leaves had withered in all treatments.

Discussion

Timing of forage senescence is influential in setting the nutritional plane for large herbivores, with the isolated effect of soil moisture potentially playing a key role in onset and rate of senescence (Livensperger et al. 2019). We found that extreme increases in soil moisture affected the senescence period of three Arctic plant species but in different ways. The grass *Alopecurus ovatus* significantly delayed senescence in the water-saturated treatment, whereas the forb *Bistorta vivipara* and dwarf shrub *Salix polaris* experienced earlier senescence in response to the same treatment. Irrespective of treatment, *Bistorta* and *Salix* had senesced by early September, at a time when green biomass of *Alopecurus* was still present in all treatments. This may explain why graminoids are an important resource for herbivores at the tail of the Arctic growth season (Hiltunen et al. 2022).

There is evidence that growth of some alpine plants is time constrained such that advanced onset of the growing season leads to earlier onset of senescence, suggesting these species have a development cycle to best

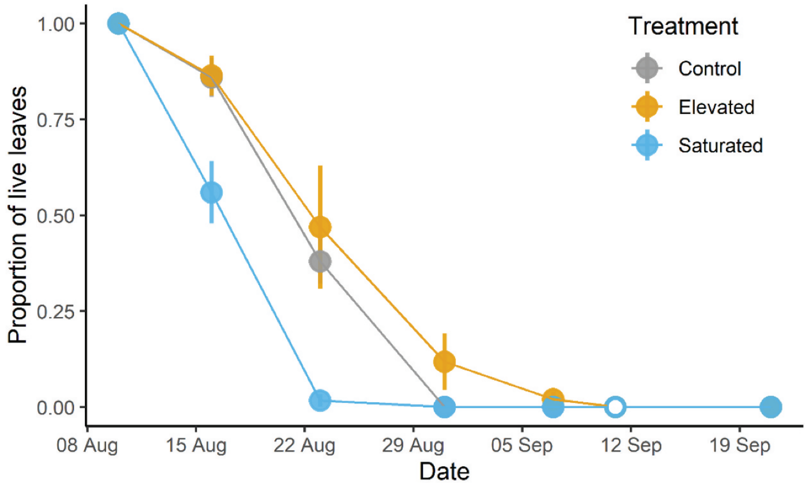

Figure 4. Effects of experimental soil moisture treatments on the mean proportion of live leaves of *Bistorta vivipara* during August and September ("saturated" in blue, "elevated" in orange, "control" in grey). Points are raw means and error bars are ±1 SE. The open circles represent the week where measurements could only be recorded for one block, with data extrapolated from other weeks to calculate an approximate mean.

exploit a short growing season (Möhl, von Büren, and Hiltbrunner 2022). Yet, we found that *rate* of senescence is flexible and responsive to soil moisture in some species, especially in our focal graminoid. Livensperger et al. (2019) also found that higher soil moisture levels generally delayed *onset* of senescence, though the effect varied between years and species, and its influence on *rate* of senescence was even more variable (with both accelerated and decelerated rates of senescence varying among years). In line with our study, soil moisture, at its extreme, can have varying effects on plant phenology, including growth. For example, waterlogging can increase biomass of graminoids (*Poa* and *Deschampsia* spp.; Person and Ruess 2003), whereas *Bistorta* and some *Salix* species struggle in water-saturated conditions (Thorhallsdottir 1993; Fan et al. 2018). This highlights the importance of soil moisture levels for plant growth and senescence in the Arctic and the need for species-specific studies.

While there was a tendency that *Bistorta* and *Salix* responded positively to elevated soil moisture by delaying senescence, the far strongest response was to saturated conditions. Although none of the focal species have aerenchyma, a common morphological adaptation to reduce stress under anoxic conditions (Iversen et al. 2015), it is possible that *Alopecurus* was able to take better advantage of waterlogging compared to *Bistorta* and *Salix* due to physiological differences. A plant's root system is highly sensitive to oxygen deprivation, and plants generally cannot sustain their growth under anoxic conditions for long (Armstrong, Brändle, and Jackson 1994; Jackson, Ishizawa, and Ito 2009). Much of our understanding of arctic species' responses to fluctuating water tables is grounded in the work of Robert Crawford (1996), who stated: "Leaves are usually the last organs to be inundated by rising water levels and the first to show adverse effects from flooding" (18). He identified, however, that populations of some common high-Arctic plant species in Svalbard had a surprisingly high anoxia tolerance (Crawford, Chapman, and Hodge 1994), though tests on more southern populations from Norway, Iceland and Scotland failed to detect such tolerance (Crawford 1996). When exposing plants from Svalbard to anoxic conditions for seven days, *Bistorta* was found to be intolerant (i.e. dies on re-exposure to air), whereas *Salix* was able to produce new leaves from anoxia-tolerant buds (Crawford, Chapman, and Hodge 1994). *Alopecurus* was not included in these laboratory tests but added to the list of anoxia-tolerant species two years later (Crawford 1996). Unlike *Bistorta*, roots of *Alopecurus* and *Salix* form extensive belowground networks throughout and below the moss layer (Brooker and Van der Wal 2003); however, in Svalbard, wet and poorly drained areas are more likely to include *Alopecurus* than *Salix* (R.vdW., pers. obs.). It may be the numerous budding ramets high up in the moss mat and the relatively tall (live and dead) aboveground stem material that facilitate gas exchange and allow *Alopecurus* to tolerate prolonged periods of inundation. Graminoids also have a fast growth rate, which often makes them better at exploiting changing resources, especially compared to *Salix* species (Person and Ruess 2003). This could explain why *Alopecurus* was the only species in our study to extend its growing season in the saturated soil moisture treatment and suggests that it could be a species more resilient to waterlogging promoted by hydrological shifts driven by climate change. Conversely, the immediate response of *Salix* and *Bistorta* could imply that they suffered from root anoxia at a sensitive time—that is, when autumn senescence is about to commence—but alternatively could point to more general sensitivity to flooding, also if occurring earlier in the growth season.

Graminoids make up the bulk of species favoured for grazing during summer and early winter by Svalbard reindeer, with *Bistorta* and *Salix* supporting the diet particularly in summer and late winter, respectively (Bjørkvoll et al. 2009). Studying the effects of climate change on these plants is therefore important to predict the future population dynamics of this large herbivore in a warmer, wetter Arctic. Graminoids are of particular interest because blood isotope analysis indicated a near-linear increase of grass in the winter diet of Svalbard reindeer between 1995 and 2012 (Hiltunen et al. 2022). We have shown that under extreme soil moisture conditions, the graminoid *Alopecurus* was the most resilient of the three study species, because it alone was able to delay senescence. Because winter starvation is the main cause of death for Svalbard reindeer (Albon et al. 2017), access to high-quality forage for a longer period of time results in larger fat reserves that in turn improve survival rates (Tews, Ferguson, and Fahrig 2007; Albon et al. 2017; Loe et al. 2021). Food limitations naturally increase towards the winter season, and though *Bistorta* and *Salix* experienced accelerated rates of senescence under continuously wet conditions, this was only by roughly one week compared to the control treatment. The strong positive effect on late-season *Alopecurus* biomass may be enough to counterweight the negative effect on *Bistorta* and *Salix*, creating a net positive effect on available biomass for the reindeer during autumn.

Conclusions

Climate change develops rapidly in the Arctic, influencing tundra ecosystems in numerous ways, including through its hydrology (Hanssen-Bauer et al. 2019). Soil moisture is one of the main structuring forces of tundra vegetation (Walker et al. 2016; Kemppinen et al. 2019). Longer-term changes in water availability in the landscape are therefore likely to cause shifts in the distribution, abundance, productivity and phenology of plant species and their assemblages, the effects of which will in turn propagate through ecosystems and food webs (Hodkinson et al. 1999; Van der Wal and Hessen 2009). For Svalbard reindeer, which are mostly food limited and bottom-up regulated, such changes are likely to affect their distribution and ability to build up energy reserves before the winter. Understanding processes affecting food availability in the autumn season is therefore of key importance, and here we have shown that waterlogging of soil is a significant contributing factor influencing timing and rate of autumn senescence. Due to the heterogeneity of the effects of climate change in the Arctic, future studies should investigate how soil moisture levels are changing at local scales and across different landscapes. Such insights will aid in understanding how plant communities may shift with climate change as well as how this may affect the abundance and distribution of Arctic herbivores such as reindeer.

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