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Autumn senescence response to a changing climate: effects of snow-depth on High Arctic plants

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Cover photo: Autumn senescence in August 2013 in Adventdalen, Svalbard. Species shown are *Cassiope tetragona*, *Dryas octopetala*, *Pedicularis hirsuta,* and *Salix polaris*.

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Note

This thesis is presented as a short version resembling a manuscript with the aim of publishing in the near future. It will be co-authored by my co-supervisor (Prof. Bo Elberling) and supervisor (Prof. Elisabeth J. Cooper) as second and third authors, respectively. All additional text is put in the appendix under "Supplementary Information" and other relevant figures in the "Additional Figures" section. Research has been conducted at Prof. Elisabeth J. Cooper's snow fence experiment in Adventdalen from 2006 and senescence data analyzed for this thesis was collected by previous members of her research group from 2008-2012, as well as during my own fieldwork this past summer in 2013.

Abstract

Temperature and precipitation in the Arctic are projected to increase over the next century with a changing climate. Understanding how tundra plants respond to this change is still unclear. Little is known about autumn senescence in the Arctic and with a short growing season, timing is critical. If a plant senesces too early, it compromises photosynthetic activity and growth. If a plant senesces too late, it risks losing nutrients to frost damage, limiting next year's growth and reproductive success. This study aims to determine the relationship between the timing of autumn senescence with different snow regimes, in particular, investigating its effects on the day of year, season length, and thawing degree day. Since 2006, snow fences have been used to experimentally manipulate snow-depth in Adventdalen, Svalbard (78°N). Between 2008-2013, the timing of senescence was recorded in eight species: *Alopecurus magellanicus, Bistorta vivipara, Cassiope tetragona, Dryas octopetala, Luzula confusa, Pedicularis hirsuta, Salix polaris,* and *Stellaria longipes* spp. *longipes* subjected to four winter snow treatments (shallow, ambient, medium and deep). The day of snowmelt in the deep (with a snow-depth of ~150 cm) treatment was consistently later than the medium (60-100 cm), ambient (10-35 cm) and shallow (1-5 cm) treatments. In general, later snowmelt resulted in delayed senescence during both senescence start (1-24% of the leaves senesced) and senescence 50 (50-74% of the leaves senesced). All species showed the same treatment effect except for *Stellaria longipes* ssp. *longipes*. Delayed snowmelt reduced the season length and the timing of senescence was unrelated to thawing degree days except in the shallow treatment. In conclusion, the timing of senescence was directly influenced by the snow regimes tested, and the consequences of early and delayed senescence may pose challenges to Arctic plants in the next century.

Keywords: Arctic, climate change, day of year, season length, senescence, snow, thawing degree day, Svalbard.

Introduction

Predicted climate change scenarios demonstrate that increases in surface temperature and precipitation will occur over the next 100 years; however, as a result of polar amplification caused by the Atlantic Meridional Overturning, the Arctic is predicted to experience the highest degree of this change (Collins *et al*. 2013). Precipitation in the Arctic occurs most often during the winter months falling as snow and melting later in the spring season, resulting in a very short growing season. Recent studies have shown that winter changes have greater implications on summer processes than originally thought (Cooper 2010). Morgner *et al*. (2010) indicated that deep snow in a snowmelt manipulation experiment in Svalbard increased the net winter CO_2 efflux in comparison to the ambient treatment. Winter soil respiration was largely controlled by snow-depth, since deeper snow insulated the ground from the cold winter air temperatures, additionally respiration can also be indirectly affected by the high soil organic matter found in some vegetation types, such as *Salix polaris* (Elberling 2007). Under deep snow, the soil surface temperature ranges from about -5°C to 0°C, which is warm enough to sustain winter respiration by microbial activity (Morgner *et al*. 2010). In the summer, deep snow plots melt out 1-2 weeks later than the control plots, delaying green-up and reducing the growing season length (Cooper *et al*. 2011). Delayed melt-out dates related to increased snow cover can result in steep vegetation gradients where productivity is decreased; however, many plants require snow banks for protection against harsh winter temperatures and desiccation (Billings & Bliss 1959). Different snow-depth treatments also altered flower abundance in two Arctic plant species, *Cassiope tetragona* and *Stellaria longipes* (syn. *crassipes*) (Semenchuk *et al.* 2013). Recognizing how these predicted changes in climate will impact summer phenology, such as green-up, flowering, senescence, and seed dispersal is beginning to be understood (Cooper *et al*. 2011).

Plant phenology, primarily flowering, has been commonly studied world-wide, though much is still unknown about the most vibrant phenophase of all: autumn senescence. Autumn leaf senescence is a fundamental process in which transport and remobilization of nutrients in the above-ground biomass is stored for next year's growth (Fracheboud *et al*. 2009; Keskitalo *et al*. 2005; Lim *et al*. 2007). Leaves undergo systematic changes in cell structure, metabolism, and gene expression, in order to breakdown and convert macromolecules into transportable compounds (Keskitalo *et al*. 2005; Lim *et al*. 2007). In perennial plants, these nutrients are stored primarily in the rhizomes, although woody and evergreen species may store nutrients in the bark, stem and/or roots (Couturier *et al*. 2010; Fracheboud *et al*. 2009). During the autumn season, the timing of leaf senescence is a trade-off between carbon acquisition and nitrogen storage; when the growing season is short, timing is critical. If a plant senesces too early, it compromises photosynthetic activity, growth and carbon acquisition (Cooper *et al.* 2011; Fracheboud *et al*. 2009; Zhao *et al*. 2012). If a plant senesces too late, it risks losing nutrients to frost damage, consequently limiting next year's growth and reproductive success (Fracheboud *et al*. 2009; Zhao *et al*. 2012). Autumn colour change begins by the preferential degradation of chloroplasts, removing the green colour from the leaf beginning at the apex and moving inwards towards the petiole (Keskitalo *et al*. 2005; See Appendix C, Fig. 20). The leaves appear yellow or orange as a result of carotenoids, which will begin to degrade following the chloroplasts (Keskitalo *et al*. 2005). Without the chloroplasts, the leaves are at risk of photo-oxidative stress, and in some species, anthocyanin concentrations will increase to protect the leaves from excess light, turning the leaves red until the final stage of leaf abscission (Keskitalo *et al*. 2005).

Previous studies at lower latitudes have indicated that senescence is solely triggered by the shortening photoperiod, specifically, the shorter days and longer nights (Arrom & Munné-Bosch 2012; Fracheboud *et al*. 2009). However, a study conducted in Northeast

Greenland revealed that senescence can be delayed by experimental warming and for this reason, photoperiod may not be the primary cause of senescence, as typically found in lower latitudes (Marchand *et al*. 2004). In contrast, a study on tundra plants in Greenland reduced the photoperiod from 24 to 8 hours which induced premature leaf senescence (Biebl 1967, as cited in McGraw *et al*. 1983). Chilling stress in cotton, *Gossypium hirsutum*, has been found to temporarily impair leaf physiology, but normalized when warmer temperatures were recovered (Zhao *et al*. 2012). Ozone (a phytotoxic air pollutant) was also found to increase foliar senescence in some tree and crop species by inducing senescent-related nutrient processes. (Burkart *et al*. 2012; Rämö *et al*. 2006; Ribas *et al*. 2005; Sanz *et al*. 2013). Leaf senescence occurring before the autumn season can be caused by drought, salinity stress, herbivory and pathogen infection (Abreu & Munné-Bosch 2008; Arrom & Munné-Bosch 2012; Ghanem *et al*. 2008; Munné-Bosch & Alegre 2004).

The primary initiator of autumn senescence in the Arctic is still unclear, making it difficult to predict how climatic changes could potentially impact such a critical component of short and long-term plant survival. The purpose of this study is to determine the relationship between the timing of autumn senescence with (a) day of year, (b) season length, and (c) thawing degree days (TDD) in eight species of Arctic plants subject to different snow-depths and melt-out dates. Additionally, senescence phases and other factors such as moisture and nitrogen (since past data is available) will be discussed in order to effectively investigate this topic in great depth. This study was carried out in a long-term snow manipulation experiment that started in 2006. The underlying hypothesis is that autumn leaf senescence may be delayed with increasing snow cover and delayed snowmelt; with a species-specific response as seen at the snow fences in other phenology studies (Cooper *et al*. 2011; Rumpf *et al*. 2014; Semenchuk *et al*. 2013).

Methods

Site Description

This study was conducted in Adventdalen (78°17´N, 16°07´E), a glacial valley located 12 km east of Longyearbyen in Spitsbergen, Svalbard (Semenchuk *et al*. 2013; See Appendix A, Fig. 11). During the summer months, the sun is above the horizon for 24-hours until the end of August. The mean monthly temperature was -5.2 °C with the warmest temperature reaching 8.2°C in the month of July, and the coldest temperature, -23.3°C in the month of March (1976-2013, Longyearbyen Airport, Svalbard: http://www.eklima.no). The annual precipitation and mean winter snow-depth was 217 mm and 16 cm respectively (1976-2013, Longyearbyen Airport, Svalbard: http://www.eklima.no). The local bedrock is Carboniferous-Cretaceous platform covered strata with sedimentary rocks overlain by aeolian and fluvial deposits (Hjelle 1993; Tolgensbakk *et al*. 2000). The micro-topography is largely shaped by the continuous permafrost, which has an active layer of 0.8 to 2.5 m deep subject to seasonal freeze and thaw cycles (Humlum *et al.* 2003). The two vegetation types investigated were heath and meadow. Heaths were largely influenced by solifluction and were located at the foot of mountain slopes or in rocky soils (Morgner *et al*. 2010). The dominating species in order of abundance were *Cassiope tetragona*, *Dryas octopetala*, *Salix polaris*, *Alopecurus magellanicus,* and *Bistorta vivipara* (Cooper *et al*. 2011). Meadows were flat, often moister than heaths, and situated adjacent to river beds (Morgner *et al*. 2010). The dominating species were *Salix polaris, Luzula confusa*, *Alopecurus magellanicus*, *Dryas octopetala,* and *Bistorta vivipara* (Cooper *et al*. 2011). Meadows had a greater moss cover, were warmer in May and June, and became snow free before heaths (Cooper *et al*. 2011). Human activity in Adventdalen consisted primarily of hikers during the summer and hunters during the autumn months. Svalbard reindeer were present year round while Barnacle and Pink-Footed geese were present during the pre-breeding season.

Experimental Design

In the autumn of 2006, twelve wooden snow fences (1.5 m high x 6.2 m long) were erected in an area spanning approximately 2.5 x 1.5 km and were positioned perpendicular to the predominating south-easterly winter wind. The fences were designed to capture snow on the leeward side by reducing the wind speed, resulting in snow deposition. The snow drift behind each fence was 1.5 m deep, 20-30 m long and decreased in depth away from each fence. The fences were situated 500 m apart and divided into four blocks of three fences (200 x 200 m), with six fences representing a vegetation type, heath or meadow (See Appendix A, Fig. 12). Experimental and natural snow-depths were used to create a high to low depth gradient where four treatments were investigated in 181 plots where each plot was 75 x 75 cm (Table 1). In the control and deep plots, three plots consisted of *Cassiope tetragona* and the other three of *Dryas octopetala* to ensure that all species were included in each treatment (See Appendix A, Fig. 13).

Eight species of vascular plants were selected that dominated the landscape and were part of the International Tundra Experiment (ITEX) (Cooper *et al*. 2010). The study species were *Alopecurus magellanicus* Lam., *Bistorta vivipara* (L.) Delarbre, *Cassiope tetragona* (L.) D. Don, *Dryas octopetala* L., *Luzula confusa* Lindeb., *Pedicularis hirsuta* L., *Salix polaris* Wahlenb., and *Stellaria longipes* ssp. *longipes* Goldie (Retrieved [May 7, 2014], from the Integrated Taxonomic Information System on-line database, http://www.itis.gov.). Species distribution varied per treatment where *Alopecurus*, *Bistorta, Dryas, Luzula* and *Salix*, were common in all the treatments, while *Cassiope* and *Stellaria* were uncommon in the shallow treatments and *Pedicularis* was uncommon in the deep treatment (See Appendix B, Fig. 16). Leaf senescence was recorded by locating all individuals per species and visually estimating the percent of senescence in each plot (0%, 1-24%, 25-49%, 50-74%, 75-99%, 100%). For simplicity, each percentage was given a name, 0% - green, 1-25% - start, 25-49% -

senescence 25, 50-74% - senescence 50, 75-99% - senescence 75, and 100% is senescence 100. Leaf senescence was recorded weekly from 2008-2012, noting the time it took to reach senescence 50 in all years, and senescence start in 2008-2010. In 2013, all phases of senescence were recorded twice a week (See Appendix A, Fig. 14). Leaf degradation was observed to have started at the apex and continued inwards until all the leaves were dead and brown, and this occurred for all leaves within the plot. Colours exhibited during senescence were yellow, red, orange, and purple depending on the species. Most species turned one or two different colours before senescence was complete. *Bistorta*, *Luzula*, *Pedicularis* and *Salix* turned yellow and red, while *Dryas* turned yellow, orange and red. *Alopecurus* and *Stellaria* turned purple and red, whereas *Cassiope* turned only purple although old growth from past years remained yellow and red. Colour changes associated with diseased or infected leaves were ignored for all species, but were noted for a further study in *Cassiope tetragona*. Senescence data was recorded for ambient and deep snow treatments from 2008-2013, and the shallow and medium snow treatments from 2010-2013.

Gemini Tiny Tag Plus 2 data loggers were installed to measure the surface temperature of the soil every hour (probe at approximately 1 cm from the surface) at each treatment per fence. Data loggers were placed at the ambient and deep treatments in 2007, and at the medium and shallow (at 10 of the 12 fences) in 2010. Batteries were changed and the logger data downloaded at the end of every summer. Melt-out dates in 2010-2012 were recorded visually in mid-May. Melt-out dates in 2008, 2009 and 2013 were determined by comparing temperature data with known melt-out dates from 2010-2012, and by using the zero curtain to indicate melt-out; which was when latent heat was absorbed after a phase change from snow to water (Kelley & Weaver 1969). This maintained a constant 0°C temperature that was visually apparent in the logger temperature data. All temperature data was checked and adjusted if necessary, using the zero curtain for calibration. Thawing degree days (TDD) were determined by averaging and then summing the daily positive temperatures from snowmelt to senescence 50 for each plot. For more details, see Cooper *et al*. (2011) and Semenchuk *et al*. (2013).

Statistical Analyses

Analyses were conducted in the statistical program R, version 3.0.3 (R Development Core Team 2014). Day of year, day of snowmelt and season length were analyzed using the senescence 50 phase. Senescence start, senescence 50, day of snowmelt, season length and TDD were analyzed using Linear Mixed Models (package lme4, hmisc, and lmerTest) testing when available, each treatment, year and species separately and together (Semenchuk *et al*. 2013; Nakagawa & Cuthill 2007). The effect size and confidence intervals were used to determine biological significance between treatments; however, to maintain standardization the standard error, t-values and p-values were also included (Nakagawa & Cuthill 2007, Tables 3-9). Because the data collected in 2008 and 2009 only contained two treatments (ambient, deep), two analyses were conducted: one with the "all treatments" (shallow, ambient, medium, deep) dataset collected in 2010-2013, and the other with "all years" dataset collected in 2008-2013 with only two treatments (ambient, deep). Senescence start was collected less frequently from 2008-2010, and in 2013 for the "all year" dataset, and 2010 and 2013 for the "all treatment" dataset. Data from 2013 was collected twice/week, whereas data in past years was collected once/week. For comparative purposes, 2013 data was scaled down to once/week using the day of year most similar to past data collections for the "all treatments" and "all years" datasets except when investigating the senescence phases. Data from 2013 was used to examine the timing of each senescence phase (senescence start, 25, 50, 75, 100), TDD, and it was excluded in the species analysis of *Alopecurus*, *Cassiope* and *Stellaria* since they did not all reach senescence 50 by the end of the sampling period (August 29th). Because the sampling period began on the first of August, plots that had reached senescence start earlier, where not used in the analysis and only species that were seen to be previously green were used to prevent an overestimation on the initial start date. Normalcy was found using the Anderson-Darling test (since n > 5000) and was visually shown using a Q-Q plot, histogram and a residual plot for each dataset. Differences between species were determined by using the most accurate dataset and phase with the largest sample size, which was during senescence 50. The importance of year was determined by using year as a single random effect and observing the standard deviation, effect size and confidence intervals. An Analysis of Variance (ANOVA) determined that species and year have interactive effects and p-values were calculated using an ANOVA. The fixed effects in the model were Day of Year ~ Treatment*Year. The random effects were (1|fence/block/plot). A similar model was used to determine the snowmelt date, season length and TDD substituting ”Day of Year” with the corresponding dataset.

Results

Climate

Climate data from the Svalbard Airport (eKlima.no), during the summer period of June 1st - August 31st, shows the differences between the years for temperature, precipitation, humidity, number of days of overcast, and the snow-depth from January 1st- May 31st (Table 2). The air temperature ranged from 4.9 to 6.3 °C, and the precipitation from 8 to 41 mm a month (Table 2). Relative humidity ranged between 71-77% and was seemingly unrelated to the amount of precipitation each summer (Table 2). Days of overcast weather ranged from 34 to 67 days and the snow-depth from 9 to 20 cm (Table 2). In the spring, the snow melted earliest in the shallow treatment followed by the ambient, medium, and lastly the deep treatment (Table 3). Senescence start and senescence 50 began the earliest in the shallow treatment and followed the same treatment effect (Table 3). Season length, defined as the number of days from snowmelt to senescence 50, was the longest in the shallow treatment and gradually increased with increasing snow-depth (Table 3). The thawing degree days in 2013, was the highest in the ambient treatment and the lowest in the deep (Table 3).

Day of Year

Senescence start and senescence 50 (effect size ± se) were delayed by an increasing snow-depth for both the “all years” and “all treatments” datasets with the shallow first, followed by the ambient, medium, and deep treatment (Fig. 1 & 2). Senescence start and senescence 50 were both delayed, on average, by 17 days from the shallow to the deep treatment (Table 3). The sampling period in 2013 started on August 1st and ended on August 29th, instead of starting in mid July and ending in mid September as in previous years, thus the senescence start and senescence 100 date may not be as representative as other years. In the senescence start "all years" dataset (excluding 2013), the ambient and deep snow-depth treatments differed by a minimum of 5 days (Fig. 1). During the "all treatments" dataset, the treatment effect in the ambient and deep snow-depth treatments differed from 1 to 11 days depending on the year, the shallow and deep from 3 to 15 days, and the ambient and medium from 1 to 4 days (Fig. 1). Overlap was present between the medium and deep treatments in 2013 (Table 4). Senescence 50 showed a similar trend, during the "all years" dataset; the ambient and deep snow-depth treatments differed by 5 to 14 days (Fig. 2). In the "all treatments" dataset the shallow and ambient differed from 1 to 6 days with some overlap in 2012 and 2013, while the ambient and medium ranged from 1 to 7 days, and the medium and deep from 2 to 4 days (Fig. 2). Overlap between treatments was present in 2011 in the medium and deep treatments, and in 2012 and 2013 in the shallow, ambient and medium treatments (Table 5). The "all years" and “all treatments” datasets both showed delayed senescence due to increasing snow-depth, but exhibited different yearly patterns of senescence start and senescence 50. Senescence start began the earliest in 2010 in both datasets, whereas senescence 50 in the “all years” dataset began the earliest in 2009 in the ambient treatment and 2008 during the deep treatment; and varied by each treatment in the “all treatments” dataset (Fig. 1 & 2).

Large standard error bars in some years could be caused by a small sample size in the shallow and medium treatments or the short sampling period in 2013 (August 2nd – August 29th). Environmental stressors such as competition, disease, herbivory, and flooding, which was present in some plots, may also impact the timing of senescence. For example, some *Salix* individuals had scattered insect galls on the leaves, which may have induced premature senescence in some individuals, as well as the pathogen *Exobasidium* spp. was present in *Cassiope tetragona* in 45 of 181 plots excluding the shallow treatment (field data, not shown).

Plant-Specific Trends

All species generally showed delayed senescence with increasing snow-depth and snowmelt date except for *Stellaria longipes* (Fig. 3 & 4). At senescence 50 in the “all years” dataset, two species, *Dryas octopetala* and *Salix polaris,* followed the same treatment effect as seen when combining the species altogether (Fig. 3D & 3G). Senescence start and senescence 50 dates in 2013 in *Alopecurus magellanicus*, *Cassiope tetragona* and *Stellaria* were not used in the analysis, since not all plots reached senescence 50. *Alopecurus* differed from 1 to 21 days and from 5 to 11 days later in the ambient and deep treatments respectively (Fig. 3A). *Bistorta vivipara* senesced earlier in the ambient treatment in 2010, but generally followed the all species treatment effect beginning slightly earlier than most species (Fig. 3B). *Cassiope tetragona* senesced very late in 2010, though still followed the all species treatment effect (Fig. 2 & 3C). *Luzula confusa* senesced much earlier altogether, though generally followed the treatment effect except in 2010 in the ambient, and in 2011 in the deep treatment (Fig. 3E). *Pedicularis hirsuta* reached senescence 50 earlier then most species in the deep treatment, though the treatments overlapped in 2010 (Fig. 3F; Table 3). *Stellaria longipes* showed the smallest treatment effect of all the species and senesced the latest (Fig. 3H). The species in the senescence 50 “all treatments” dataset followed the same treatment and yearly trends in the “all years” dataset, exhibiting delayed senescence with an increasing snow-depth (Fig. 4). *Alopecurus* behaved similarly in the shallow, ambient and medium treatments, and was delayed in the deep treatment from 3 to 23 days (Fig. 4A). *Bistorta* acted identically in the shallow and ambient treatments, and showed little difference in the medium and deep treatments (Fig. 4). Senescence 50 in *Cassiope* overlapped regardless of the treatment (Fig. 4C; Table 7). *Salix* and *Dryas* displayed the all species treatment effect; however, greater overlap was present between the shallow and ambient treatments in all years (Fig. 4D & 4G; Table 7). Similarly, *Luzula* senesced later in deeper snow; however, all the treatments overlapped in 2011 (Fig. 4E; Table 7). *Pedicularis* showed the least pronounced treatment effect whereas *Stellaria* showed little difference between years, with an increased treatment effect over time (Fig. 4F & 4H).

Senescence Phase

The senescence phases showed a less pronounced treatment effect, than compared to senescence start and senescence 50 over many years, and ranged from August 16th (228) to August 25th (237) (Fig. 5). This may be due to the shorter field season in 2013; however, in the deep treatment senescence 100 was reached more rapidly than at other phases (Fig. 5; Table 8). The senescence phases were not constant throughout, but the trend was not affected by the snow treatments, only delayed (Fig. 5). Once senescence began, senescence 25 followed 0-2 days after senescence start (Fig. 5). This could be due to the difficulty in distinguishing between senescence start and 25 in plots containing individuals at both phases. Senescence phase 50, 75, and 100 occurred 1 to 5 days, 5 to 7 days and 1 to 8 days later, respectively (Fig. 5).

Snowmelt Date and Season Length

The day of year of snowmelt was later with increasing snow-depth, and followed a similar yearly pattern between the day of snowmelt and senescence 50, specifically in the "all treatments" dataset (Fig. 2). An earlier snowmelt occurred in 2010 that had little impact on the timing of senescence 50 in the medium and deep treatments (Fig. 2). The relationship between the day of year to reach senescence 50 and the day of year of snowmelt showed a treatment effect, especially in the "all years" dataset; and the same was present in the "all treatments" dataset except with overlap between the shallow and medium treatments (Fig. 6; Table 6). The season length followed the snow treatment effect and the yearly variation corresponded to the day of snowmelt except for the overlap in 2011 (Fig. 7). The season length during the "all years" dataset ranged from 70 to 86 days in the ambient, and 60 to 75 days in the deep treatment (Fig. 7). In the "all treatments" dataset, the season length greatly overlapped in each treatment, and the deep treatment showed almost no yearly effect (Fig. 7; Table 9). The relationship between the day of year to reach senescence 50 and season length depicts a positive trend indicating that the timing of senescence 50 was delayed with increasing season length (Fig. 8).

Thawing Degree Days

The relationship between the day of year to reach senescence 50 and the thawing degree days (TDD) was unrelated and only showed a distinct trend in the shallow treatment (Fig. 9). The TDD were very similar per treatment, where the shallow ranged from 380 to 720 °C, ambient from 470 to 755 °C, medium from 480 to 790 °C, and the deep treatment from 277 to 700 °C (Fig. 9). The relationship between the season length and the TDD primarily ranged from 475-660 °C with a season length between 73 and 84 days in all treatments, but it was difficult to discern a clear treatment effect (Fig. 10).

Other Factors

Moisture data collected at the snow fences was measured during 2007 and 2008 (See Appendix C, Fig. 15 & 17). The moisture content was highest after snowmelt and decreased by approximately 62% after 2.5 weeks (See Appendix C, Fig. 15 & 17). The carbon to nitrogen ratio (C:N) in *Salix* plots were determined from July 20th - September 14th, 2012 (See Appendix C, Fig. 18). The ambient treatment had a C:N ratio of 14 to 21.5, and the deep treatment from 11 to 14 for the first five weeks (July 20th – August 22nd). After the fifth week (August 22nd), of which senescence 50 began, the carbon to nitrogen ratio increased rapidly and was 46% more in the ambient and 44% in the deep by the eighth week (September 14th).

Discussion

Day of Year

In all datasets, both senescence start and senescence 50 exhibited a snow treatment effect, in which plants reached senescence earlier in the shallow plots and later as the snow-depth increased (Fig. 1 & 2). A previous study on plant phenology at the snow fences in Advendalen, Svalbard indicated that senescence was delayed on average by 6 days in the deep snow treatment (Cooper *et al*. 2011). Initially, the quality of light (red and far-red) was assumed to be the primary driver of senescence at all latitudes. A study conducted on European Aspen (*Populus tremula*) tested the date of senescence with different light regimes and concluded that senescence in *P. tremula* was driven by a shortened photoperiod and could be accelerated by a decreasing temperature and longer nights; however, populations vary by latitude as well as the timing of bud set and growth arrest (Fracheboud *et al*. 2009). A similar study examining the cellular timetable of senescence in free-growing aspen found that photoperiod was the key driver, since temperature and precipitation remained unchanged around the time of senescence, and only the day-length fluctuated (Keskitalo *et al.* 2005). Although fewer studies have been conducted in the Arctic, these reveal, in contrast, photoperiod has little effect on autumn senescence in most cases. In Alaska, an observational study in 1977-1981, found that decreases in temperature appeared to initiate senescence regardless of the photoperiod, although the authors concluded that controlled experiments may be needed for confirmation (McGraw *et al*. 1983). Marchand *et al.* (2004) used infrared heating in Greenland and demonstrated delayed senescence or presence of prolonged greenness in plots warmed by 2.5 °C. As reported in our study, all eight species began to senesce on different dates regardless of the day-length, and followed the different snow-depth treatments (Fig. 1 & 2). A study by Biebl (1967) as cited by McGraw *et al.* (1983) changed the photoperiod from 24 hours to 8 hours and induced early leaf senescence in four alpine species in Greenland, *Betula nana, Vaccinium uliginosum, Empetrum hermaproditum,* and *Salix glauca*. Leaves of *Salix polaris* from two ecotypes, 69°N and 78°N, senesced later when exposed to a 24-hour photoperiod at 15°C and gradually senesced earlier with a reduced day-length; however, when the temperature decreased to 9 and 6°C, both ecotypes senesced much earlier, except the ecotype at 78°N was completely unaffected by the shortening day-length unlike individuals at ecotype 69°N (Paus *et al*. 1986). Thus, the timing of senescence in Arctic plants may be influenced by photoperiod when the temperature is close to 9°C. The average summer temperature of our plots ranged from 5.9 to 6.3 °C depending on the year (eKlima.no). Jones *et al*. (1997) used open-top chambers (OTCs) to experimentally warm plots by 1 to 4°C on Ellesmere Island, Canada and found that the OTCs had no impact on the yellowing of leaves in *Salix arctica*. Studies' concluding that temperature was the main cause of delayed senescence had heated plots to temperatures above 7 °C, which was confirmed in Marchand *et al*. (2004) who heated his plots from 7.90-9.26°C, whereas Jones *et al*. (1997) plots did not exceed 6.2°C with the presence of OTCs.

Although the sun never sets beyond the horizon, the irradiance and energy distribution in regards to the red to far-red ratio does change with the sun's rotation (Nilsen 1985 as cited in Jones *et al*. 1997). Photoreceptor proteins, such as phytochromes, cryptochromes and phototropins are responsible for monitoring incoming light (Tsegay *et al*. 2005), and how these proteins function during autumn senescence in Arctic species may provide an answer as to why increasing temperature may initiate a sensitivity to day-length in some cases.

Differences between years were seen in both the "all years" and "all treatments" datasets in senescence start, senescence 50, day of snowmelt and season length (Fig. 1-4 & 7). As noted in Semenchuk *et al*. (2013) in early 2010 and 2012, a winter warming event took place in which the temperature and precipitation were recorded above the 1976-2012 average. During the 2013 summer season, precipitation was also at its highest compared to the 1976-

2013 average (eKlima.no; Table 2). Generally, all species showed delayed senescence with increasing snow-depth and snowmelt date except for *Stellaria longipes*.

Alopecurus magellanicus

Senescence 50 in *Alopecurus* occurred later than in most species, in both the “all years” and “all treatments” datasets, in particular, in the ambient, medium and deep snow-depth treatments (Fig. 3A & 4A). The distribution of *Alopecurus* was found most often in the medium and deep treatments (See Appendix C, Fig. 16). In Cooper *et al*. (2011) differences between the date of senescence and seed dispersal varied by 4 to 9 days respectively, whereas green-up and flowering varied by 11 to 12 days from the ambient to the deep treatment. Our study follows a similar trend, on average from 2008-2012, the difference between the ambient and deep treatment was 9 days (Table 7). *Alopecurus* was a late senescing species which may explain why the different treatments delayed senescence by fewer days than the earlier phases (Fig. 3A & 4A).

Bistorta vivipara

Senescence 50 in *Bistorta* followed the snow-depth treatment effect; however, senescence began earlier in all treatments (Fig. 3B & 4B). *Bistorta* was distributed equally between the treatments, but was less common in Block A, which was a well-drained heath (See Appendix C, Fig. 16). Individual plants with flowers also seemed to reach senescence earlier than vegetative plants (2013 field observations, not shown). Differences in the date of senescence and flowering between the ambient and deep treatment was 7 days, but 14 days for green-up (Cooper *et al*. 2011). Since both flowering and senescence were each delayed by the same number of days, it is possible that the onset of senescence may be linked to flowering; however, more research needs to be conducted. In contrast, Starr *et al.* (2010) found that *Bistorta officinalis* (syn. *Polygonum bistorta*) in Alaska senesced at the same time when the season was extended by early snow removal, and snow removal and warming, thus was a periodic species. In our study and in Cooper *et al*. (2011), *Bistorta vivipara* senesced later with increasing snow-depth and delayed snowmelt, and did not show the same seasonal periodicity (Fig. 2, 4B & 5B).

Cassiope tetragona

Cassiope followed the overall snow treatment effect in the “all years” dataset; however, in the “all treatments” dataset the shallow and medium treatments displayed overlap (Fig. 3C & 4C). The distribution of *Cassiope* was more common in the ambient, medium, and deep treatments (See Appendix C, Fig. 16). Green-up, flowering and senescence from the ambient to the deep treatment was delayed by 6, 13, and 10 days (Cooper *et al*. 2011). *Cassiope* may be more vulnerable to a decrease in snow-depth, as seen in Semenchuk *et al*. (2013) since the winter warming event in 2010 caused a reduction in the number of flowers in the shallow treatment (See Appendix C, Fig. 21). Spring bud and leaf development in *Cassiope* was especially sensitive to frost, thus deeper snow provides protection in May when the temperatures are below 0°C (Callaghan *et al*. 1995). Blok *et al*. unpublished manuscript (2014) determined that stem growth in *C. Tetragona*, at the same snow fence experiment, increased in the deep plots and that deeper snow was essential for frost protection. However, shoot length, number of leaves, and capsules per shoot in *Cassiope* were reduced by deeper snow (Mallik *et al*. 2011). Thus, in *Cassiope,* a certain threshold of snow is required for optimal growth, and its response to different snow regimes is starting to be understood.

Dryas octopetala

Senescence 50 in *Dryas* also followed the overall treatment effect in both datasets (Fig. 2, 3D & 4D). The distribution of *Dryas* was spread evenly across all treatments, and was found to be the most prominent plant in the shallow plots (field observation, See Appendix C,

Fig. 16). In Cooper *et al*. (2011) green-up, flowering, senescence and seed dispersal was delayed by 19, 15, 9, and 1 day respectively. Flowering in *Dryas* also showed a sensitivity to the winter warming event in 2012; however, due to its compactness and low-lying flowers, it fairs well under colder temperatures in the shallow plots unlike *Cassiope* (Semenchuk *et al*. 2013). *Dryas* is a long-lived evergreen with high phenotypic plasticity and is able to better adapt to changes in the environment (Wookey *et al*. 1995).

Luzula confusa

Luzula followed the overall treatment effect, except in 2011 in both datasets and senesced earlier than most species (Fig. 2, 3E, 4E). It is also distributed evenly across treatments (See Appendix C, Fig. 16). Phenological development of *Luzula* in the deep snow treatments was delayed by 9, 7, 7 and 3 days during green-up, flowering, senescence and seed dispersal respectively (Cooper *et al*. 2011). Again, the delay between flowering and senescence was identical and thus may be related, though more research needs to be conducted.

Pedicularis hirsuta

Pedicularis senesced earlier than most species and followed the overall treatment effect most years; however, in the all treatments dataset the deep and medium plots overlapped (Fig. 3F & 4F). Distribution of *Pedicularis* was common in all treatments, but in lesser quantities in the shallow plots (See Appendix C, Fig. 16). *Pedicularis* was one of two species that was more difficult to locate in crowded plots, due to its small size and often solitary individuals. The timing of senescence was highly variable per plot, in which some individuals would be entirely green, often with no flowers present, while others would reach senescence 50 or senescence 75 all in the same plot (field observations, not shown). Interestingly, Cooper *et al*. (2011) demonstrated delayed green-up, flowering and seed dispersal by 11 days, whereas senescence was delayed by 3 days. Similarly, *Pedicularis* was found to senesce earlier than other species, and often individuals with flowers, senesced immediately. The onset of flowering in *Pedicularis* was initiated by snowmelt and depended on the degree of development in overwintering buds (Eriksen *et al*. 1993) thus the timing of snowmelt could be closely linked to the phenological development of this species.

Salix polaris

Salix followed the overall effect and was distributed equally among all treatments (Fig. 3G & 4G; See Appendix C, Fig. 16). Cooper *et al*. (2011) found in the deep treatment that *Salix* reached green-up, flowering, senescence, and seed dispersal after 14, 12, 11, and 12 days respectively, later then the ambient treatment. *Salix* spp. exposed to OTCs did not exhibit a delay in senescence or other phenological development (Jones *et al*. 1997).

Stellaria longipes

Stellaria senesced the latest of all the species and had the smallest treatment effect (Fig. 3H & 4H). The distribution of *Stellaria* was found in all treatments, but was less common in the shallow plots (See Appendix C, Fig. 16). *Stellaria* reached green-up, flowering, senescence in the deep treatment by 2, 11, and 1 day after the ambient treatment (Cooper *et al*. 2011). Notably, *Stellaria* was a late senescing species, thus the impact of the snow treatments had little or no effect on senescence. *Stellaria* is a polyploid species with high phenotypic plasticity (Macdonald & Chinnappa 1989). The timing of flowering in *Stellaria* was influenced by the different snow regimes only some in years (Semenchuk *et al.* 2013), thus *Stellaria* may be better adapted to cope with changing snow-depths than the other species.

Senescence Phase

The senescence phase showed a less pronounced treatment effect that was uniform throughout, except in the deep treatment during senescence 100. Senescence in the deep treatment had already been delayed and these results may be caused by the plant hurrying to senesce before the end of the growing season and not risking frost damage. In *Populus tremula*, leaf cells did not senesce at the same time; however, it was a synchronous process in the tree as a whole (Keskitalo *et al*. 2005). In northern Manitoba, Canada, plants subjected to different snow-depth treatments showed no change in the duration of the vegetative and reproductive phenological stages and may be controlled by intrinsic factors (Legault & Cusa 2014, unpublished manuscript). Kukavica & Jovanovic (2004) showed that antioxidants present during senescence are the same in two tree species, *Gingko biloba* and *Betula pendula*; however, the amounts can vary. This indicates that the timing of the different senescence phases may be delayed by different snow regimes, but the overall length of senescence may be intrinsically controlled and vary per species.

Snowmelt Date and Season Length

The snowmelt date was delayed with increased snow-depth and plots that melted later in the season had delayed senescence (Fig. 2 & 6). Species that preferred to live in shallow snow were at greater risk of being grazed by Svalbard reindeer since their preference for species with a high biomass and low quality were found in plots with early melt-out, such as *Luzula* and *Salix* (Van der Wal *et al*. 2000). Although senescence was delayed by later snow-melt, earlier phenological phases such as green-up and flowering exhibited a greater delay as a result of deeper snow (Cooper *et al*. 2011). This delay in other phenological phases caused by later snowmelt may be a crucial step to initiate early senescence. Sequential plant development in green-up, flowering and seed dispersal may promote earlier senescence when occurring more rapidly in the season. This was observed repeatedly in the field, in which individuals with flowers senesced earlier than individuals without flowers (field observation, not shown). Annual plants will senesce soon after flowering beginning at the shoot apical meristem, followed by the leaves and finally by suppressing axillary bud growth (Davies & Gan 2012). In agreement, Eriksen *et al*. (1993) found that reproduction in *Pedicularis hirsuta* was closely related to snowmelt date, choosing late-melting snow beds. For this reason snowmelt date may be an important contributor to plant phenology.

The season length was found to be reduced with increased snow-depth and the number of days varied per treatment (Fig. 7 & 8). In contrast to our findings, Starr *et al*. (2000) found that *Bistorta officinalis* (syn. *Polygonum bistorta*) required a similar season length to senesce regardless of the treatment (warming and extended season length); therefore, the importance of season length could be species-specific. A shorter season length was also shown to reduce reproductive success in some species in the deep snow treatment (Cooper *et al*. 2011). Similarly to snowmelt date, season length may also reduce the capacity of certain species that are not well-adapted to increased snow-depth, to produce flowers later in the season, suggesting that senescence may be more closely related to plant development than other abiotic factors.

Thawing Degree Days

The timing of senescence was found to be unrelated to thawing degree days (TDD) except in the shallow treatment (Fig. 9). Since the shallow treatment melts out the earliest, the plots may have been exposed to warmer spring temperatures which may have postponed senescence; similar to studies that found that increased warming above 7°C caused later senescence regardless of the day-length (Paus *et al*. 1986; Marchand *et al*. 2004). When combined with season length, no clear relationship was found; however, the majority of plots had a season length from 74 to 83 days with a TDD between 475 and 660 °C regardless of the treatment (Fig. 10). The cumulative degree-day sum was determined to have no effect on the timing of senescence in Alaska, and that temperature may be the primary initiator (McGraw *et al*. 1983). The growing degree days (GDD) in a snow cover experiment in Alaska found that later phenophases were influenced by GDD more so than earlier phases (Wipf 2009). Above-ground plant growth was largely affected by air temperature sums, and species with later melt-out dates were subjected to a shorter growing season and fewer positive temperatures; however, it was largely species-specific (Rumpf *et al.* 2014; See Appendix C, Fig. 19). A study looking at the geographical range of *Cassiope tetragona* at different latitudes, found that in the High Arctic, vegetative growth was limited by temperature, whereas Subarctic populations were limited by nitrogen and shading (Havström *et al*. 1993). Levesque *et al*. (1997) found that the temperature and TDD reduced with increased altitude and plots were the warmest in a valley on Ellesmere Island, Canada. Therefore, if temperature was a controlling factor, further investigation could compare the timing of senescence in areas with altitudinal differences or by warming plots above 7°C.

Other factors

The moisture content was highest after snowmelt and decreased rapidly over the summer season (See Appendix C, Fig. 15 & 17). The fence site was well-drained except in a few places where the micro-topography shifted and caused the formation of small pools of water in a couple of plots (field observation, not shown). Precipitation was the highest in the summer of 2013 compared to other years and senescence was not found to occur substantially earlier or later than drier seasons. A study by Welker *et al*. (1993) showed that the addition of water caused the leaf mass of *Dryas octopetala* to decrease possibly due to a shift in growth allocation from vegetative to reproductive. In *Bistorta*, the photosynthetic capability was increased by the addition of water, more so than by increasing nitrogen, in stomatal conductance (Enquist & Ebersole 1994). Thus, increased moisture may impact earlier phases and vegetative processes, but has not been shown to affect the timing of senescence. Though drought can be an important regulator of senescence in alpine mountainous species, Arctic tundra species did not senesce earlier with changing precipitation nor did it limit growth and species distribution in a Tussock tundra and snow patch site (McGraw *et al*. 1983; Oberbauer & Miller 1982). In agreement, Keskitalo *et al*. (2005) recorded summer precipitation during autumn senescence of which it remained unchanged.

Using preliminary data from plots containing *Salix*, the C:N ratio of the soil increased by more than half during the summer after snowmelt (See Appendix C, Fig.18). Interestingly around the time of senescence, the nitrogen content decreased more rapidly. Little is known about the function of the roots during senescence and it is possible that they could be taking in additional nitrogen from the soil in preparation for next year's growth. It is still uncertain as to how much nitrogen was produced over winter in the deep snow treatment compared to the ambient and since the soil was well-insulated under deeper snow, microbial activity and respiration will occur. Plots warmed with open-top chambers did not have an increased pool of nitrogen (Hudson *et al*. 2011). Buckeridge *et al*. (2009) found that areas with high quality litter together with low soil C and microbial activity will promote rapid soil N-cycling in the Canadian Low Arctic. Van der Wal *et al*. (2000) found that the nitrogen content of the leaves of *Luzula* declined after snowmelt. Senescent leaves in *Dryas* were found to have a higher C:N ratio in warmer and wetter conditions which makes them harder to decompose and would slow down nutrient recycling (Welker *et al*. 1997). This strategy of the leaf C:N ratio may take place to prevent the loss of nitrogen in order to pass it on to next year's growth (Welker *et al*. 1997). A study on senescence found that ozone (O_3) stimulated senescence in an annual grass species (*Bromus hordeaceous*) of which nitrogen mitigated the O_3 effect (Sanz *et al*. 2013). Further studies need to examine the nitrogen content in over-wintering plots to determine if there is a difference between treatments and how this difference may impact not only the timing of senescence, but also the timing of other phenophases.

Conclusion

Although very little is known or understood about the causes that drive autumn senescence in the Arctic, this study has attempted to integrate the mechanisms of winter and summer processes to better explain autumn senescence. In conclusion, the timing of senescence was found to be directly influenced by the different snow regimes in all species, except for in *Stellaria longipes*. Changing snow regimes can have multifactorial effects on the environment, such as changing the snowmelt date, season length, temperature, thawing degree days, moisture and nitrogen. Deeper snow delayed the snowmelt date and reduced the season length, which can alter the timing of other plant phenophases, such as green-up, flowering, and seed dispersal. The completion of these phases may induce earlier senescence in some species; however, further studies need to be conducted. The thawing degree days were unrelated to the timing of senescence, but temperatures above 7°C may promote extended greenness. In order to determine the primary initiator of senescence further studies on these factors need to be investigated further. Future climatic changes in precipitation and temperature, most certainly will have an effect on the timing of senescence as seen already, futhermore Arctic plants will need to find ways to adapt to this change. Either they will senesce earlier and lose summer productivity resulting in the arrest of carbon uptake, shifting from a carbon sink to a carbon source, or they will senesce later and risk losing nitrogen input for the following year. Regardless of how they cope with this change, this study definitively shows that senescence in the Arctic was not caused by an intrinsic factor; the timing of senescence is flexible, and plants may be able to adapt in some cases, but perhaps not in all. With projected climate change, the consequences of early and delayed senescence may pose challenges to Arctic plants in the next century.

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Figures

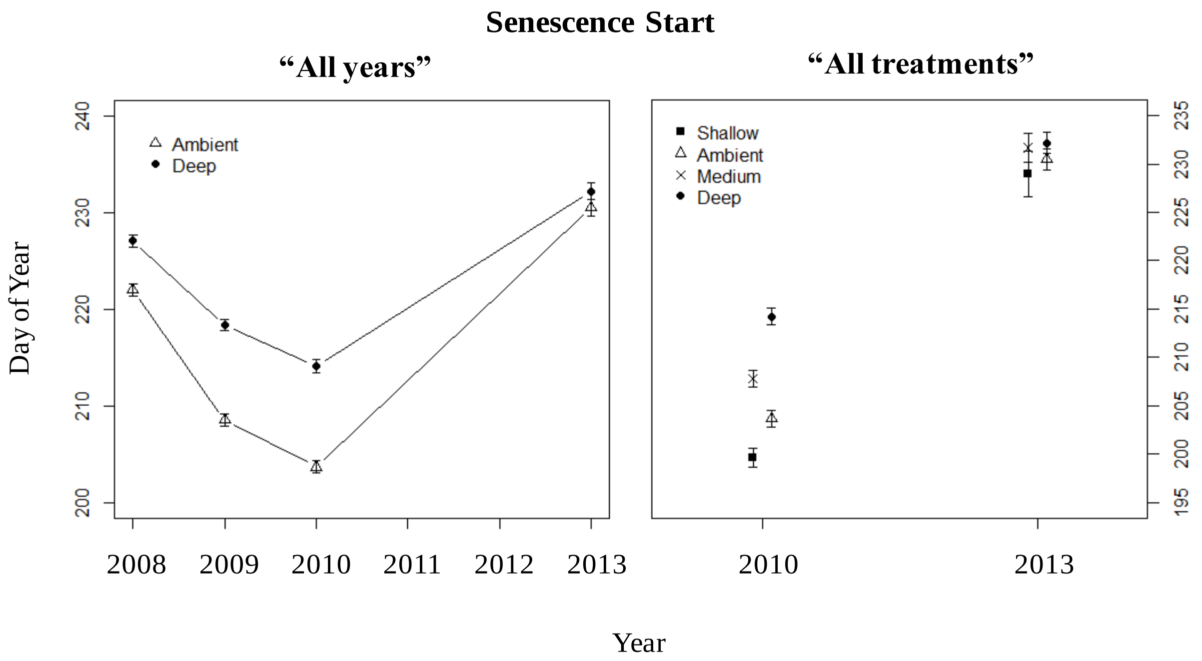

Figure 1: Day of year taken to reach senescence start (effect size ± se) for all species using the "all years" (n=2759) and “all treatments” (n=1860) datasets fitted with a linear mixed effects model.

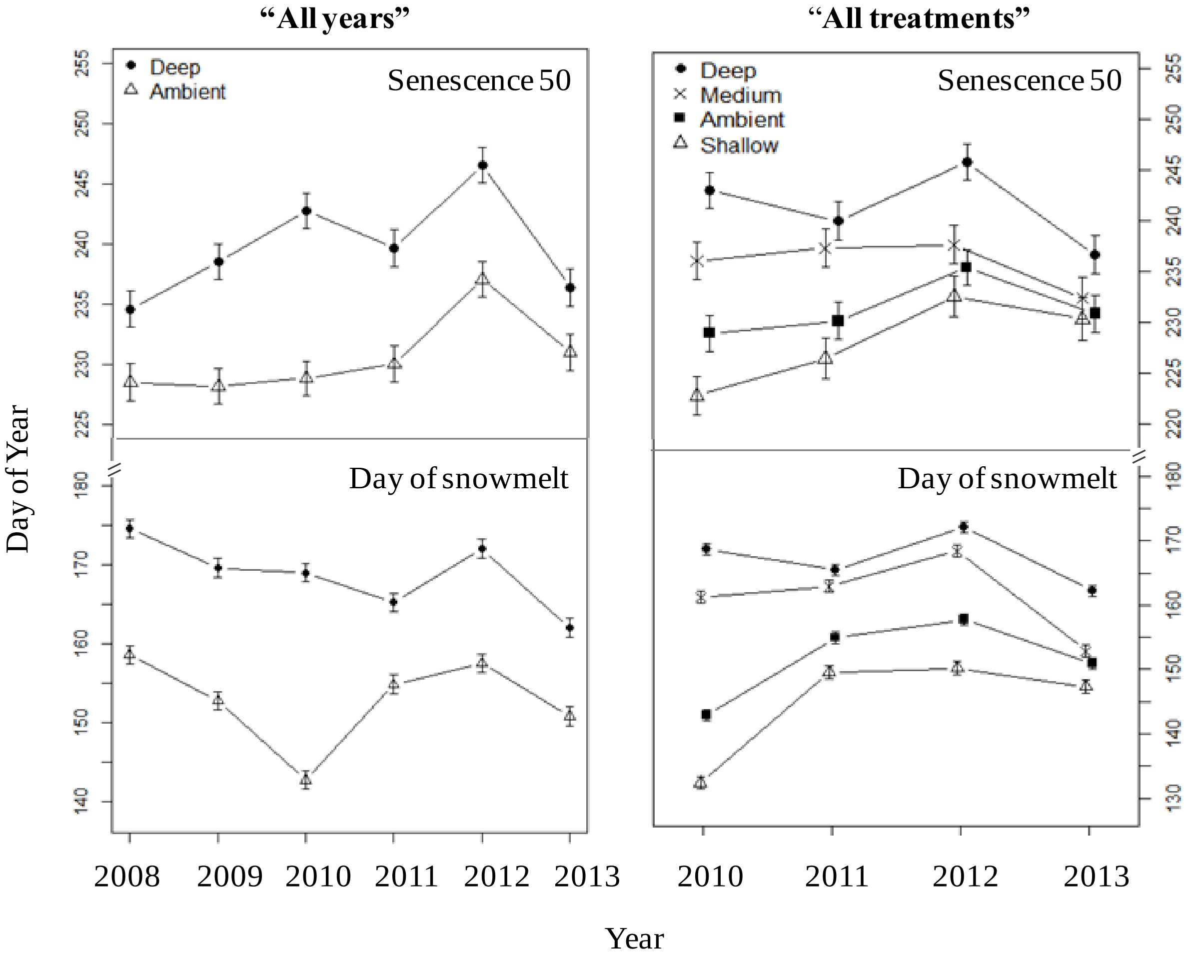

Figure 2: Day of year taken to reach senescence 50 and day of snowmelt (effect size ± se) for all species using the “all years” (n=3535) and “all treatments” (n=3843) datasets fitted with a linear mixed effects model.

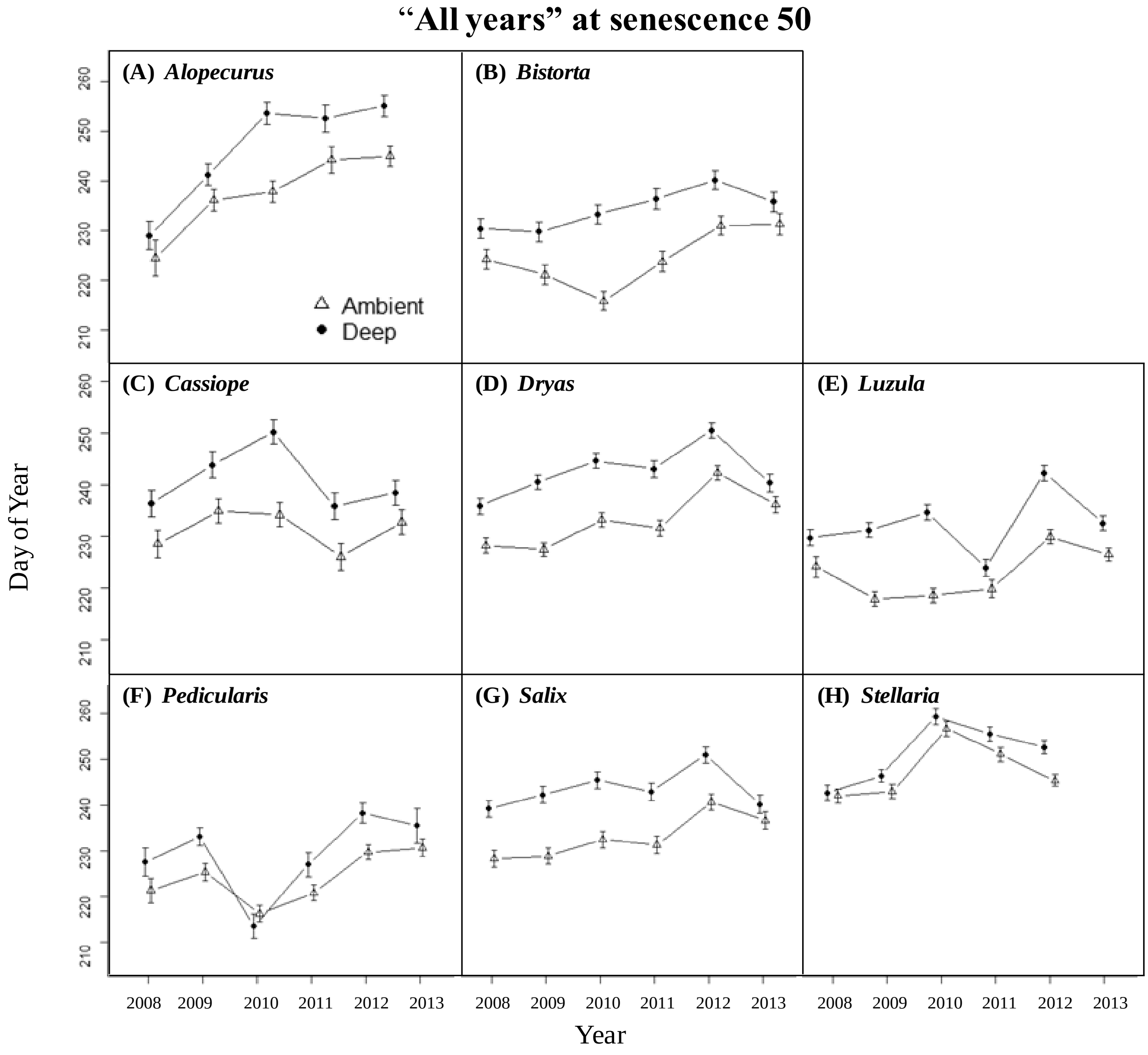

Figure 3: Day of year taken to reach senescence 50 (effect size ± se) for each species, (a) *Alopecurus magellanicus* (n=322), (b) *Bistorta vivipara* (n=595), (c) *Cassiope tetragona* (n=378), (d) *Dryas octopetala* (n=521), (e) *Luzula confusa* (n=617), (f) *Pedicularis hirsuta* (n=222), (g) *Salix polaris* (n=577), (h) *Stellaria longipes* (n=309) using the "all years" dataset with two snow-depth treatments (ambient, deep) fitted with a linear mixed effects model. Data collected in 2013 was excluded in the analysis in *Alopecurus*, *Cassiope* and *Stellaria*, since not all individuals reached senescence 50 by the end of the sampling period.

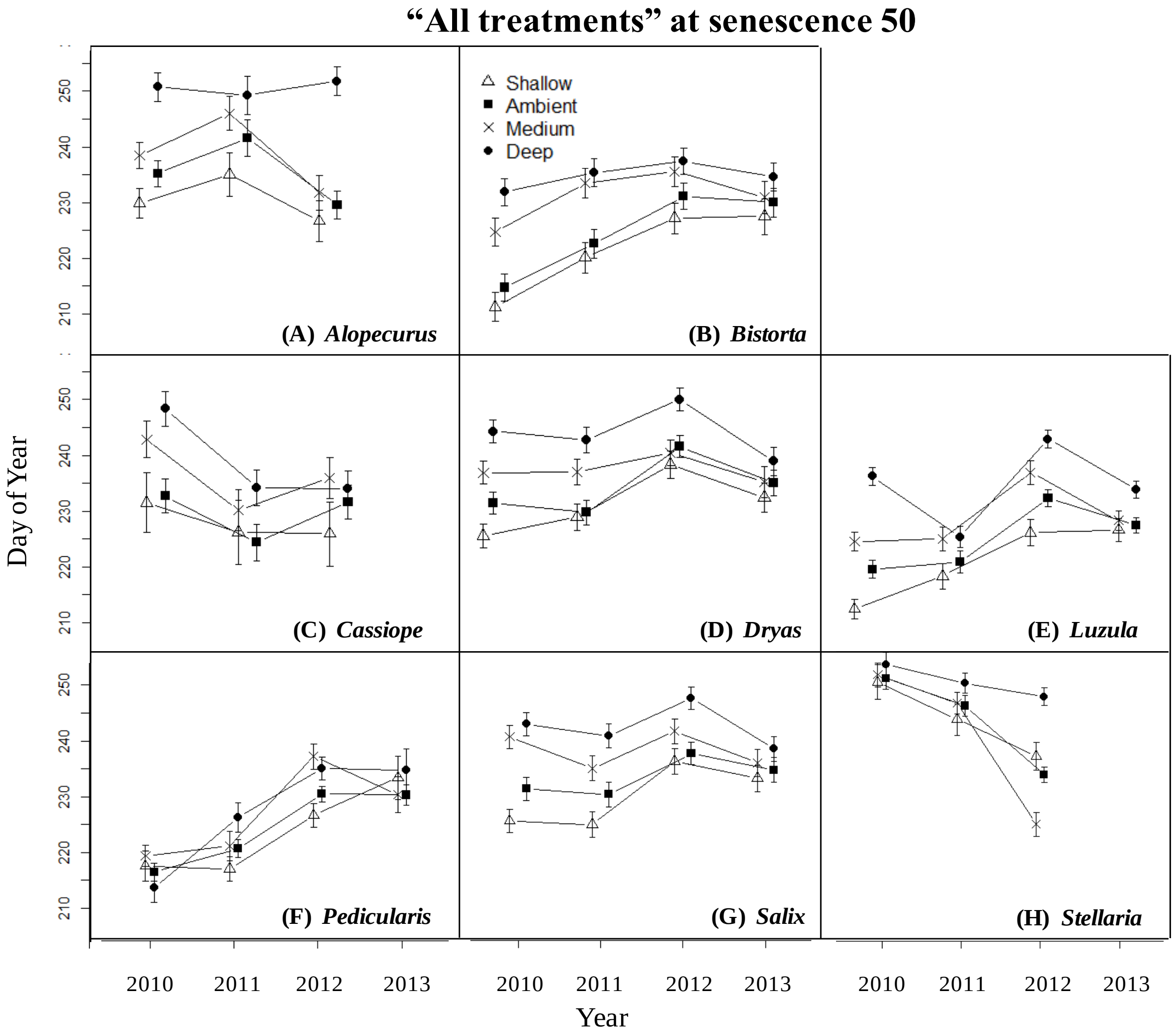

Figure 4: Day of year taken to reach senescence 50 (effect size ± se) for each species, (a) *Alopecurus magellanicus* (n=391), (b) *Bistorta vivipara* (n=666), (c) *Cassiope tetragona* (n=340), (d) *Dryas octopetala* (n=581), (e) *Luzula confusa* (n=696), (f) *Pedicularis hirsuta* (n=246), (g) *Salix polaris* (n=643), (h) *Stellaria longipes* (n=280), using the "all treatments" dataset with all snow-depth treatments (shallow, ambient, medium, deep) fitted with a linear mixed effects model. Data collected in 2013 was excluded in the analysis in *Alopecurus*, *Cassiope* and *Stellaria*, since not all individuals reached senescence 50 by the end of the sampling period.

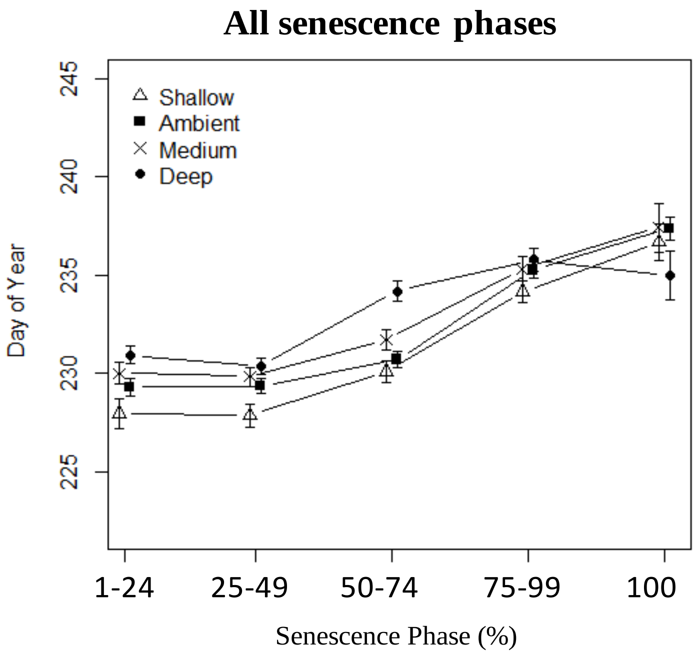

Figure 5: Day of year taken to reach each senescence phase (effect size ± se) in 2013 only, for all species and all snow-depth treatments (shallow, ambient, medium, deep) fitted with a linear mixed effects model (n=4692).

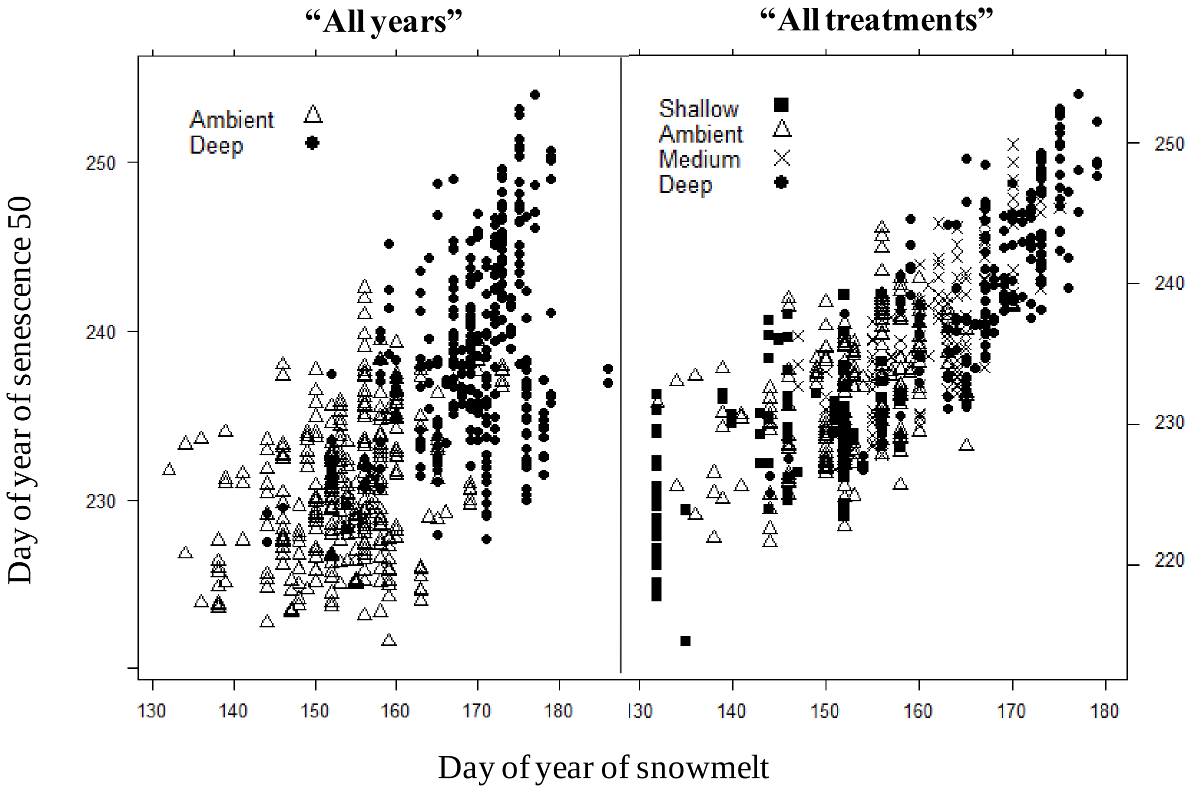

Figure 6: Relationship between the day of year to reach senescence 50 with the date of snowmelt in the "all years" and "all treatments" datasets fitted with a linear mixed effects model.

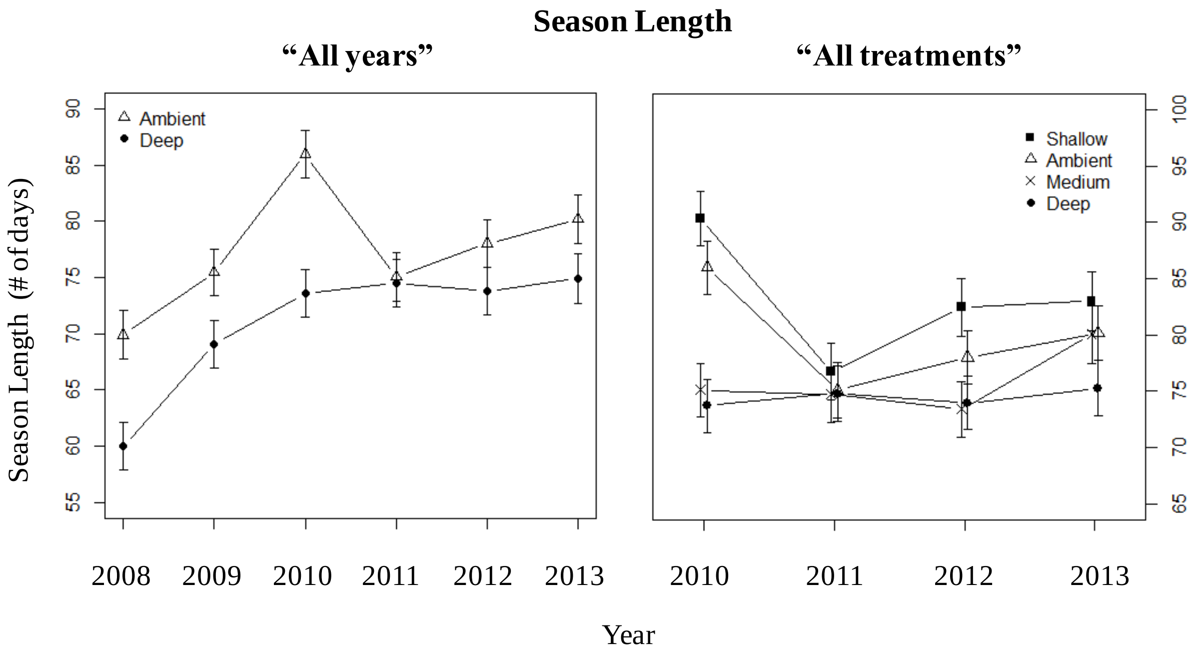

Figure 7: Season length taken to reach senescence 50 (effect size ± se) in all species using the "all years" (n=3535) and "all treatments" (n=3843) datasets fitted with a linear mixed effects model.

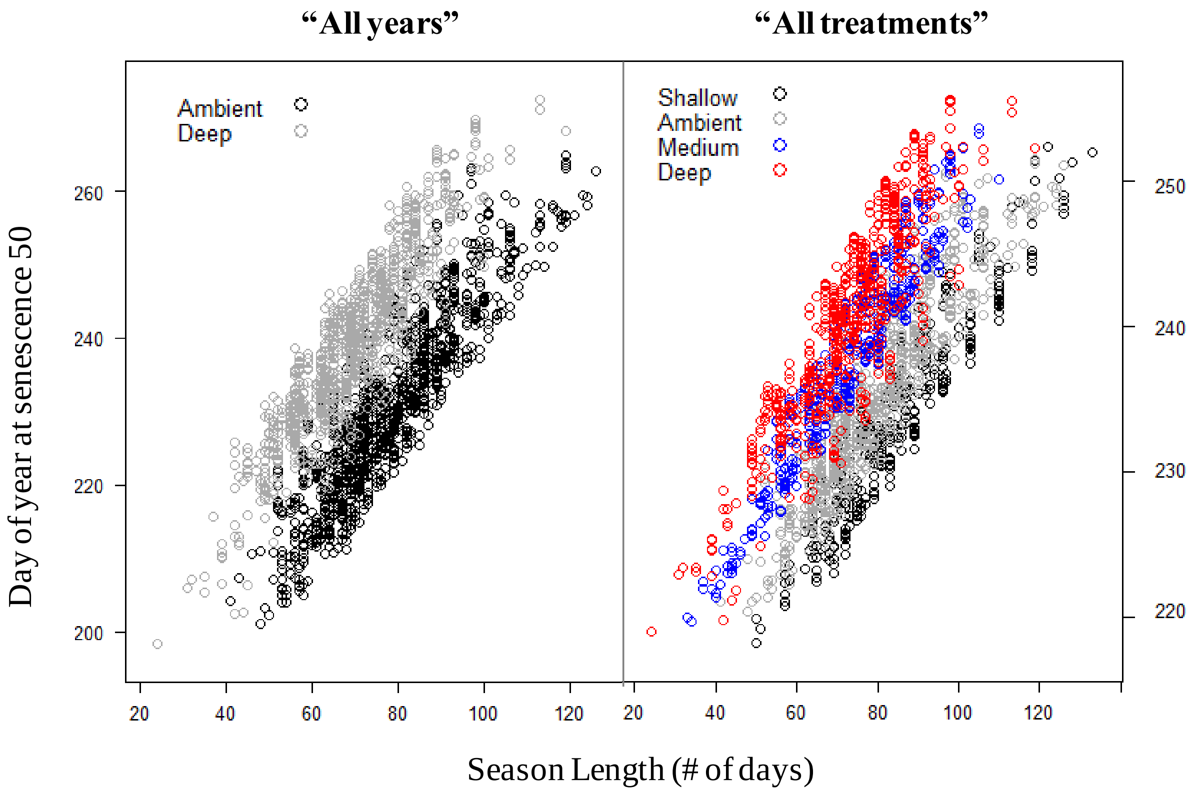

Figure 8: Relationship between the day of year to reach senescence 50 with the season length for the "all years" and "all treatments" datasets fitted with a linear mixed effects model.

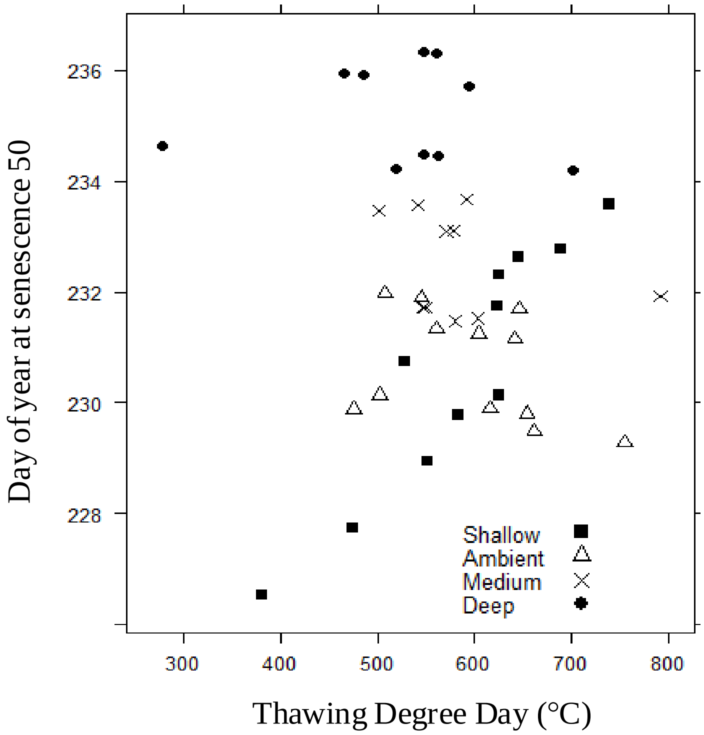

Figure 9: Relationship between the day of year to reach senescence 50 with the thawing degree days (TDD) for all snow-depth treatments (shallow, ambient, medium, deep) during 2013 fitted with a linear mixed effects model (n=579).

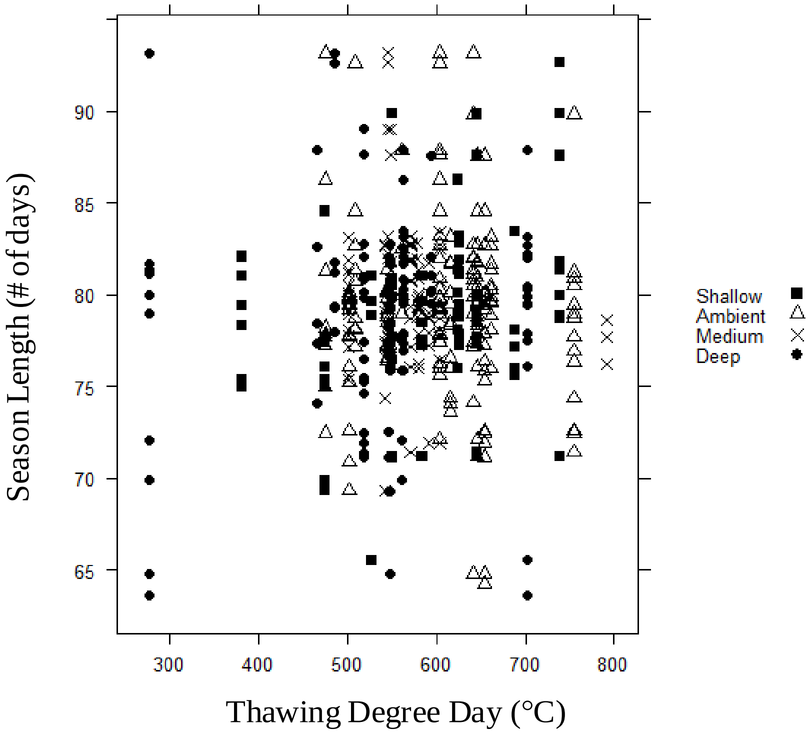

Figure 10: Relationship between the season length with the thawing degree days (TDD) for all snow-depth treatments (shallow, ambient, medium, deep) during 2013 fitted with a linear mixed effects model (n=579).

Tables

Table 1: Description of the snow cover treatments and plots in Adventdalen, Svalbard. Ambient and deep plots were established in 2007 and medium and shallow plots in 2010.

Treatment	Manipulation	Snow Depth (cm)	Nº of Plots per Fence	Plot Location
Deep	Experimental	approx. 150	6	3 - 12 m behind the fence
Medium	Experimental	60 - 100	3	approx. 10 - 20 m behind the fence
Ambient	Natural	10 - 35	6	Usually adjacent to each fence
Shallow	Natural	1 -5	2	Usually in wind-blown or ridged areas

Table 2: Climate data from the Svalbard Airport in Longyearbyen, Svalbard during 2008-2013 (http://www.eklima.no). The mean air temperature, precipitation, relative humidity and total number of days of overcast were from June 1st- August 31st, and the mean snow depth was from January 1st- May 31st.

Year	**Air Temperature (°C)**	**Precipitation (mm)**	**Humidity (%)**	**Overcast (# of days)**	**Snow Depth (cm)**
2008	4.9	17	75	40	n/a
2009	5.7	8	73	34	20
2010	5.0	10	77	43	9
2011	6.2	8	71	48	19
2012	5.4	17	73	57	6
2013	6.3	41	75	61	12

Table 3: Average snowmelt, senescence start, senescence 50 date, season length (senescence 50 – snowmelt date), and the thawing degree days for each snow treatment (shallow, ambient, medium, deep). The snowmelt date, senescence 50 and season length were averaged from 2010-2013, senescence start in 2010 and 2013, and the thawing degree days in 2013. The day of year is in brackets.

	Shallow	**Ambient**	**Medium**	**Deep**
Snowmelt Date	May 22 (142)	June 1 (152)	June 11 (162)	June 17 (168)
Senescence Start Date	July 23 (204)	July 31 (212)	August 1 (213)	August 9 (221)
Senescence 50 Date	August 16 (228)	August 20 (232)	August 24 (236)	August 30 (242)
Season Length (# of days)	85	80	75	74
Thawing Degree Days (°C)	587	609	565	541

Table 4: Effects of snow-depth treatments (fixed effect) on the timing (day of year) of senescence start in the "all treatment" and "all years" datasets for all species fitted with a linear mixed effects model.

Senescence Start	**Year**	**Effect ± se**	**Confidence Interval**	**t-value**	**p-value**
All Treatments					
Fixed Effects					
Ambient (Intercept)	2010	203.7 ± 0.8	± 1.6	245.20	<0.001
	2013	27.0 ± 1.0	± 2.1	27.00	<0.001
Shallow	2010	-4.1 ± 1.1	± 2.0	-3.69	<0.001
	2013	25.3 ± 2.7	± 4.7	9.4	0.361
Medium	2010	4.1 ± 1.0	± 2.0	4.2	<0.001
	2013	28.0 ± 2.0	± 4.0	14.0	0.138
Deep	2010	10.6 ± 1.0	± 2.0	10.8	<0.001
	2013	28.5 ± 1.7	± 2.2	16.8	<0.001
Random Effects		sd			
Plot:(Fence:Block)		0.0			
Fence:Block		0.7			
Block		0.9			
All Years					
Fixed Effects					
Ambient (Intercept)	2008	222.0 ± 0.7	± 1.3	339.3	<0.001
	2009	-13.5 ± 1.1	± 2.2	-11.8	<0.001
	2010	-18.3 ± 1.2	± 2.4	-15.4	<0.001
	2013	8.4 ± 1.5	± 1.6	5.8	<0.001
Deep	2008	5.1 ± 0.9	± 3.0	5.9	<0.001
	2009	3.63 ± 1.1	± 2.2	3.2	<0.001
	2010	7.9 ± 1.2	± 1.4	5.6	<0.001
	2013	10.2 ± 1.5	± 3.0	7.1	0.019
Random Effects		sd			
Plot:(Fence:Block)		0.7			
Fence:Block		0.7			
Block		0.0			

Table 5: Effects of snow-depth treatments (fixed effect) on the timing (day of year) of senescence 50 in the "all treatments" and "all years" datasets for all species fitted with a linear mixed effects model.

Senescence 50	**Year**	**Effect ± se**	**Confidence Interval**	**t-value**	**p-value**
All Treatments					
Fixed Effects					
Ambient (Intercept)	2010	229.0 ± 1.1	± 3.6	125.0	<0.001
	2011	1.2 ± 1.6	± 3.7	0.8	0.230
	2012	8.3 ± 1.5	± 3.5	5.5	<0.001
	2013	2.1 ± 1.7	± 3.7	1.2	0.058
Shallow	2010	-6.4 ± 1.8	± 3.8	-5.7	<0.001
	2011	-2.7 ± 1.6	± 4.0	-1.7	0.137
	2012	4.5 ± 1.5	± 4.0	3.0	0.035
	2013	1.3 ± 1.7	± 4.2	0.8	0.002
Medium	2010	7.1 ± 1.0	± 3.6	7.1	<0.001
	2011	8.3 ± 1.4	± 3.7	6.0	0.973
	2012	14.0 ± 1.3	± 3.7	10.7	0.001
	2013	3.6 ± 1.6	± 4.1	2.2	0.001
Deep	2010	13.8 ± 1.0	± 3.6	13.9	<0.001
	2011	10.7 ± 1.4	± 3.7	7.7	0.004
	2012	18.1 ± 1.3	± 3.6	13.9	0.004
	2013	7.6 ± 1.5	± 3.8	5.0	<0.001
Random Effects		sd			
Plot:(Fence:Block)		2.3			
Fence:Block		0.9			
Block		3.4			
All Years					
Fixed Effects					
Ambient (Intercept)	2008	228.6 ± 1.5	± 3.0	157.8	<0.001
	2009	-0.3 ± 1.3	± 2.7	-0.3	0.700
	2010	0.4 ± 1.3	± 2.7	0.3	0.733
	2011	1.6 ± 1.4	± 2.8	1.1	0.140
	2012	8.5 ± 1.3	± 2.6	6.6	<0.001
	2013	2.6 ± 1.5	± 2.8	1.8	0.014
Deep	2008	5.9 ± 1.1	± 2.8	5.6	<0.001
	2009	9.8 ± 1.3	± 2.7	7.6	<0.001
	2010	14.1 ± 1.3	± 2.7	10.9	<0.001
	2011	9.3 ± 1.4	± 2.8	6.5	0.013
	2012	18.0 ± 1.3	± 2.7	13.9	0.007
	2013	7.6 ± 1.5	± 3.00	5.1	0.629
Random Effects		sd			
Plot:(Fence:Block)		2.1			
Fence:Block		1.3			
Block		2.3			

Table 6: Effects of snow-depth treatments (fixed effect) per species (*Alopecurus magellanicus, Bistorta vivipara, Cassiope tetragona, Dryas octopetala, Luzula confusa, Pedicularis hirsuta, Salix polaris, Stellaria longipes*) on the timing (day of year) of senescence 50 in the "all treatments" and "all years" datasets fitted with a linear mixed effects model.

Senescence 50 for Each Species	**Year**	**Effect ± se**	**Confidence Interval**	**t-value**	**p-value**
All Treatments					
Fixed Effects - ***Alopecurus***					
Ambient (Intercept)	2010	237.9 ± 2.4	± 4.8	98.0	<0.001
	2011	6.3 ± 4.1	± 5.9	1.5	0.070
	2012	6.6 ± 3.4	± 4.8	1.9	0.045
Shallow	2010	-5.8 ± 2.6	± 5.3	-2.2	0.075
	2011	-0.8 ± 4.4	± 6.9	-0.2	0.827
	2012	4.4 ± 3.9	± 6.6	1.1	0.625
Medium	2010	3.1 ± 2.3	± 4.7	1.3	0.229
	2011	10.3 ± 3.8	± 5.6	2.7	0.812
	2012	10.2 ± 3.5	± 5.8	2.9	0.798
Deep	2010	15.2 ± 2.5	± 5.0	6.1	<0.001
	2011	14.3 ± 4.1	± 6.1	3.5	0.128
	2012	15.0 ± 3.4	± 5.0	4.4	0.109
Random Effects		sd			
Plot:(Fence:Block)		0.0			
Fence:Block		2.8			
Block		2.2			
All Years					
Fixed Effects - ***Alopecurus***					
Ambient (Intercept)	2008	224.5 ± 3.7	± 7.2	61.2	<0.001
	2009	11.7 ± 2.2	± 4.3	5.3	0.002
	2010	13.4 ± 2.1	± 4.2	6.4	<0.001
	2011	19.7 ± 2.6	± 5.2	7.6	<0.001
	2012	20.5 ± 2.1	± 4.3	9.8	<0.001
Deep	2008	4.5 ± 2.8	± 5.7	1.6	0.277
	2009	16.8 ± 2.1	± 4.3	8.0	0.890
	2010	29.1 ± 2.2	± 4.4	13.2	0.014
	2011	28.1 ± 2.7	± 2.7	10.4	0.446
	2012	30.7 ± 2.2	± 4.4	14.0	0.215
Random Effects		sd			
Plot:(Fence:Block)		2.8			
Fence:Block		1.8			
Block		2.8			
All Treatments					
Fixed Effects - ***Bistorta***					
Ambient (Intercept)	2010	215. 9 ± 2.4	± 4.9	9.0	<0.001
	2011	8.0 ± 2.6	± 5.2	3.1	<0.001
	2012	16.5 ± 2.4	± 4.9	6.9	<0.001
	2013	15.4 ± 2.6	± 5.3	5.9	<0.001
Shallow	2010	-3.5 ± 2.6	± 5.2	-1.4	0.041
	2011	5.4 ± 2.8	± 5.6	1.9	0.708
	2012	12.5 ± 2.8	± 5.6	4.5	0.829
	2013	12.5 ± 3.3	± 6.5	3.8	0.760
Medium	2010	10.0 ± 2.5	± 5.0	4.0	<0.001
	2011	18.9 ± 2.7	± 5.4	7.0	0.710

	2012	21.0 ± 2.7	± 5.4	7.8	0.012
	2013	16.3 ± 2.9	± 5.8	5.6	<0.001
Deep	2010	17.3 ± 2.5	± 4.9	6.9	<0.001
	2011	20.8 ± 2.6	± 5.2	8.0	0.049
	2012	22.9 ± 2.4	± 4.9	9.5	<0.001
	2013	20.1 ± 2.5	± 5.1	8.0	<0.001
Random Effects		sd			
Plot:(Fence:Block)		3.3			
Fence:Block		2.3			
Block		4.2			
All Years					
Fixed Effects - ***Bistorta***					
Ambient (Intercept)	2008	224.2 ± 2.0	± 4.1	112.1	<0.001
	2009	-3.2 ± 2.0	± 4.0	-1.6	0.041
	2010	-8.4 ± 1.9	± 3.8	-4.4	<0.001
	2011	-0.5 ± 2.1	± 4.1	-0.2	0.778
	2012	1.9 ± 1.9	± 3.8	1.0	<0.001
	2013	2.1 ± 2.1	± 4.2	1.0	<0.001
Deep	2008	6.2 ± 2.0	± 4.0	3.1	<0.001
	2009	5.5 ± 2.0	± 3.9	2.8	0.234
	2010	9.1 ± 2.0	± 3.8	4.6	<0.001
	2011	6.0 ± 2.0	± 4.1	3.0	0.004
	2012	16.0 ± 1.9	± 3.8	8.4	0.116
	2013	11.6 ± 2.0	± 4.0	5.8	0.459
Random Effects		sd			
Plot:(Fence:Block)		2.6			
Fence:Block		1.6			
Block		3.2			
All Treatments					
Fixed Effects - ***Cassiope***					
Ambient (Intercept)	2010	234.5 ± 3.0	± 6.0	78.2	<0.001
	2011	-8.3 ± 3.2	± 6.5	-2.6	0.001
	2012	-1.0 ± 3.0	± 6.0	-0.4	0.628
Shallow	2010	-1.2 ± 5.3	± 10.5	-0.2	0.810
	2011	-6.5 ± 5.7	± 11.4	-1.1	0.646
	2012	-6.7 ± 5.7	± 11.4	-1.2	0.491
Medium	2010	10.1 ± 3.2	± 6.5	3.1	<0.001
	2011	-2.6 ± 3.7	± 7.3	-0.7	0.252
	2012	3.2 ± 3.6	± 7.2	0.9	0.108
Deep	2010	15.5 ± 3.0	± 6.1	5.2	<0.001
	2011	1.5 ± 3.2	± 6.4	0.5	0.089
	2012	1.4 ± 3.1	± 6.2	0.4	<0.001
Random Effects		sd			
Plot:(Fence:Block)		5.2			
Fence:Block		2.0			
Block		4.8			
All Years					
Fixed Effects - ***Cassiope***					
Ambient (Intercept)	2008	228.6 ± 2.7	± 5.4	84.7	<0.001
	2009	6.4 ± 2.4	± 4.8	2.7	0.008
	2010	5.6 ± 2.3	± 4.6	2.4	0.016
	2011	-2.5 ± 2.6	± 5.2	-1.0	0.326
	2012	4.2 ± 2.4	± 4.7	1.8	0.075
Deep	2008	7.8 ± 2.6	± 5.3	3.0	0.004
	2009	15.3 ± 2.5	± 4.9	6.1	0.745

	2010	21.7 ± 2.4	± 4.7	9.0	0.012
	2011	7.3 ± 2.5	± 5.0	2.9	0.579
	2012	10.1 ± 2.4	± 4.9	4.2	0.520
Random Effects		sd			
Plot:(Fence:Block)		3.4			
Fence:Block		1.0			
Block		3.6			
All Treatments					
Fixed Effects - ***Dryas***					
Ambient (Intercept)	2010	232.7 ± 1.9	± 3.9	122.5	<0.001
	2011	-1.6 ± 2.1	± 4.3	-0.8	0.307
	2012	9.8 ± 1.9	± 3.8	5.2	<0.001
	2013	3.5 ± 2.3	± 4.6	1.5	0.065
Shallow	2010	-5.7 ± 2.1	± 4.2	-2.7	0.001
	2011	-2.4 ± 2.4	± 4.7	-1.0	0.052
	2012	6.7 ± 2.4	± 4.7	2.8	0.289
	2013	1.0 ± 2.5	± 5.1	0.4	0.265
Medium	2010	5.3 ± 2.0	± 3.9	2.7	0.001
	2011	5.5 ± 2.2	± 4.5	2.5	0.445
	2012	8.7 ± 2.3	± 4.5	3.8	0.005
	2013	3.7 ± 2.7	± 5.4	1.4	0.085
Deep	2010	12.5 ± 2.0	± 4.1	6.3	<0.001
	2011	11.0 ± 2.3	± 4.5	4.8	0.940
	2012	18.0 ± 2.0	± 4.1	9.0	0.052
	2013	7.3 ± 2.4	± 4.9	3.0	0.003
Random Effects		sd			
Plot:(Fence:Block)		3.6			
Fence:Block		0.6			
Block		3.1			
All Years					
Fixed Effects - ***Dryas***					
Ambient (Intercept)	2008	227.4 ± 1.5	± 3.0	151.6	<0.001
	2009	-0.8 ± 1.4	± 2.8	-0.6	0.492
	2010	5.3 ± 1.4	± 2.8	3.8	<0.001
	2011	3.6 ± 1.6	± 3.2	2.3	0.012
	2012	14.9 ± 1.4	± 2.8	10.6	<0.001
	2013	1.7 ± 1.7	± 3.4	1.0	<0.001
Deep	2008	8.1 ± 1.6	± 3.2	5.1	<0.001
	2009	13.1 ± 1.5	± 3.0	8.7	0.002
	2010	17.4 ± 1.5	± 3.0	11.6	0.033
	2011	15.8 ± 1.7	± 3.4	9.3	0.057
	2012	23.7 ± 1.5	± 3.0	15.8	0.732
	2013	12.9 ± 1.8	± 3.7	7.2	0.133
Random Effects		sd			
Plot:(Fence:Block)		4.1			
Fence:Block		0.5			
Block		2.1			
All Treatments					
Fixed Effects - ***Luzula***					
Ambient (Intercept)	2010	219.0 ± 1.7	± 3.3	128.8	<0.001
	2011	1.4 ± 2.0	± 4.1	0.7	0.516
	2012	13.2 ± 1.6	± 3.2	8.3	<0.001
	2013	8.2 ± 1.4	± 2.8	5.9	<0.001
Shallow	2010	-7.4 ± 1.8	± 3.7	-4.1	<0.001
	2011	-1.3 ± 2.4	± 4.7	-0.6	0.149

	2012	6.8 ± 2.5	± 4.9	2.7	0.761
	2013	7.3 ± 2.1	± 4.2	3.5	0.018
Medium	2010	5.2 ± 1.8	± 3.5	2.9	0.008
	2011	5.6 ± 2.2	± 4.5	2.5	0.768
	2012	18.0 ± 2.2	± 4.4	8.2	0.894
	2013	9.1 ± 1.8	± 3.6	5.0	0.086
Deep	2010	17.3 ± 1.7	± 3.4	10.2	<0.001
	2011	6.0 ± 1.9	± 3.9	3.2	<0.001
	2012	24.2 ± 1.7	± 3.4	14.2	0.013
	2013	14.8 ± 1.6	± 3.3	9.2	<0.001
Random Effects		sd			
Plot:(Fence:Block)		2.5			
Fence:Block		0.0			
Block		2.0			
All Years					
Fixed Effects - ***Luzula***					
Ambient (Intercept)	2008	225.0 ± 2.1	± 4.2	107.2	<0.001
	2009	-6.6 ± 1.5	± 2.9	-4.4	0.003
	2010	-5.9 ± 1.5	± 3.0	-3.9	0.009
	2011	-4.5 ± 1.9	± 3.7	-2.4	0.069
	2012	6.0 ± 1.4	± 2.9	4.3	0.006
	2013	2.4 ± 1.3	± 2.5	1.9	0.249
Deep	2008	5.9 ± 1.6	± 3.2	3.7	0.015
	2009	7.4 ± 1.5	± 3.0	4.9	0.005
	2010	11.0 ± 1.5	± 3.0	7.3	<0.001
	2011	-0.3 ± 1.7	± 3.5	-0.2	0.615
	2012	19.0 ± 1.5	± 3.1	12.6	0.014
	2013	8.8 ± 1.5	± 2.9	5.9	0.855
Random Effects		sd			
Plot:(Fence:Block)		3.3			
Fence:Block		0.0			
Block		1.6			
All Treatments					
Fixed Effects - ***Pedicularis***					
Ambient (Intercept)	2010	216.1 ± 1.8	± 3.5	120.0	<0.001
	2011	4.5 ± 1.7	± 3.4	2.7	0.037
	2012	15.1 ± 1.5	± 2.9	10.1	<0.001
	2013	14.9 ± 1.9	± 3.9	7.9	<0.001
Shallow	2010	1.1 ± 3.0	± 6.0	0.4	0.727
	2011	0.6 ± 2.4	± 4.8	0.3	0.231
	2012	11.0 ± 2.3	± 4.7	4.8	0.199
	2013	18.3 ± 4.2	± 8.3	4.4	0.690
Medium	2010	3.1 ± 2.1	± 4.2	1.5	0.203
	2011	5.0 ± 2.9	± 5.7	1.7	0.497
	2012	22.4 ± 2.4	± 4.8	9.3	0.243
	2013	15.0 ± 3.5	± 6.9	4.3	0.495
Deep	2010	-3.1 ± 2.9	± 5.7	-1.1	0.332
	2011	10.6 ± 2.8	± 5.7	3.8	0.038
	2012	20.1 ± 2.2	± 4.5	9.2	0.041
	2013	19.8 ± 4.2	± 8.3	4.7	0.147
Random Effects		sd			
Plot:(Fence:Block)		7.2e-7			
Fence:Block		2.9			
Block		0.0			
All Years					

Fixed Effects - ***Pedicularis***					
Ambient (Intercept)	2008	221.3 ± 2.7	± 5.4	82.0	<0.001
	2009	4.0 ± 1.9	± 3.9	2.1	0.158
	2010	-5.1 ± 1.8	± 3.6	-2.9	0.063
	2011	-0.5 ± 1.8	± 3.6	-0.3	0.843
	2012	8.4 ± 1.6	± 3.2	16.8	0.002
	2013	9.3 ± 2.0	± 3.9	4.7	0.001
Deep	2008	6.2 ± 3.2	± 6.3	1.9	0.100
	2009	11.7 ± 1.9	± 3.9	6.2	0.719
	2010	-7.8 ± 2.7	± 5.4	-2.9	0.056
	2011	5.7 ± 2.7	± 5.4	2.1	0.998
	2012	16.9 ± 2.2	± 4.4	7.7	0.590
	2013	14.2 ± 3.8	± 7.6	3.8	0.809
Random Effects		sd			
Plot:(Fence:Block)		0.0			
Fence:Block		3.6			
Block		1.2			
All Treatments					
Fixed Effects - ***Salix***					
Ambient (Intercept)	2010	232.7 ± 2.3	± 4.5	101.2	<0.001
	2011	-1.1 ± 2.4	± 4.8	-0.5	0.435
	2012	7.0 ± 2.3	± 4.5	3.0	<0.001
	2013	3.7 ± 2.5	± 5.0	1.5	0.015
Shallow	2010	-6.3 ± 2.4	± 4.7	-2.6	<0.001
	2011	-7.1 ± 2.5	± 5.1	-2.8	0.877
	2012	5.5 ± 2.6	± 5.1	2.1	0.018
	2013	2.1 ± 2.6	± 5.2	0.8	0.046
Medium	2010	10.3 ± 2.3	± 4.6	4.5	<0.001
	2011	4.1 ± 2.5	± 4.9	1.6	0.012
	2012	11.4 ± 2.5	± 4.9	4.6	0.002
	2013	5.1 ± 2.6	± 5.3	2.0	<0.001
Deep	2010	12.8 ± 2.3	± 4.9	5.6	<0.001
	2011	10.5 ± 2.4	± 4.6	4.4	0.531
	2012	17.9 ± 2.3	± 4.8	7.8	0.284
	2013	7.9 ± 2.5	± 4.5	3.2	<0.001
Random Effects		sd			
Plot:(Fence:Block)		2.9			
Fence:Block		2.0			
Block		4.0			
All Years					
Fixed Effects - ***Salix***					
Ambient (Intercept)	2008	228.2 ± 1.8	± 3.6	190.2	<0.001
	2009	0.5 ± 1.8	± 3.6	0.3	0.633
	2010	4.1 ± 1.8	± 3.6	2.3	<0.001
	2011	3.0 ± 1.9	± 3.8	1.6	0.017
	2012	12.3 ± 1.8	± 3.5	6.8	<0.001
	2013	8.3 ± 1.9	± 3.9	4.3	<0.001
Deep	2008	10.8 ± 1.9	± 3.7	5.7	<0.001
	2009	13.9 ± 1.8	± 3.6	7.7	0.117
	2010	17.0 ± 1.7	± 3.6	10.0	0.179
	2011	14.5 ± 1.9	± 3.8	7.6	0.668
	2012	22.6 ± 1.8	± 3.6	12.6	0.716
	2013	11.8 ± 2.0	± 3.9	5.9	<0.001
Random Effects		sd			
Plot:(Fence:Block)		2.7			

Fence:Block		1.7			
Block		3.1			
All Treatments					
Fixed Effects - ***Stellaria***					
Ambient (Intercept)	2010	256.8 ± 2.3	± 4.5	111.6	<0.001
	2011	-5.7 ± 2.2	± 4.3	-2.6	0.063
	2012	-19.8 ± 1.6	± 3.1	-12.4	<0.001
Shallow	2010	-0.8 ± 3.6	± 7.2	-0.2	0.846
	2011	-7.8 ± 3.3	± 6.5	-2.4	0.727
	2012	-16.0 ± 2.9	± 5.8	-5.5	0.381
Medium	2010	0.7 ± 2.5	± 5.0	0.3	0.841
	2011	-5.2 ± 2.2	± 4.5	-2.4	0.972
	2012	-30.0 ± 2.5	± 5.0	-12.0	0.013
Deep	2010	2.8 ± 2.5	± 5.0	1.1	0.407
	2011	-1.1 ± 2.1	± 4.1	-0.5	0.676
	2012	-3.8 ± 1.8	± 3.7	-2.1	0.001
Random Effects		sd			
Plot:(Fence:Block)		0.0			
Fence:Block		1.8			
Block		0.2			
All Years					
Fixed Effects - ***Stellaria***					
Ambient (Intercept)	2008	242.0 ± 1.5	± 3.0	161.3	<0.001
	2009	0.9 ± 1.5	± 3.0	0.6	0.579
	2010	14.7 ± 1.6	± 3.2	9.2	<0.001
	2011	9.1 ± 1.5	± 3.1	6.1	<0.001
	2012	3.4 ± 1.3	± 2.6	2.6	0.022
Deep	2008	0.6 ± 1.6	± 3.2	0.4	0.714
	2009	4.4 ± 1.4	± 2.8	3.2	0.212
	2010	17.3 ± 1.7	± 3.4	10.2	0.454
	2011	13.5 ± 1.5	± 3.0	9.0	0.121
	2012	10.7 ± 1.4	± 2.8	7.6	0.003
Random Effects		sd			
Plot:(Fence:Block)		1.5			
Fence:Block		1.5			
Block		1.7			

Table 6: Effects of snow-depth treatments (fixed effect) on the senescence phase (1-24%, 25-49%, 50-74%, 75-99%, 100%) in the "all treatments" and "all years" datasets for all plant species fitted with a linear mixed effects model.

Senescence Phase	**Phase**	**Effect ± se**	**Confidence Interval**	**t-value**	**p-value**
All Treatments					
Fixed Effects					
Ambient (Intercept)	1-24	229.3 ± 0.5	± 1.0	458.6	<0.001
	25-49	0.0 ± 0.4	± 0.8	0.1	0.904
	50-74	1.4 ± 0.4	± 0.9	3.5	<0.001
	75-99	5.9 ± 0.4	± 0.9	14.9	<0.001
	100	8.0 ± 0.6	± 1.2	13.4	<0.001
Shallow	1-24	-1.4 ± 0.8	± 1.5	-1.7	0.070
	25-49	-1.5 ± 0.6	± 1.1	-2.4	0.866
	50-74	0.8 ± 0.5	± 1.1	1.6	0.405
	75-99	4.8 ± 0.6	± 1.1	8.1	0.777
	100	7.4 ± 0.9	± 1.8	8.2	0.583
Medium	1-24	0.7 ± 0.5	± 1.1	1.4	0.184
	25-49	0.5 ± 0.5	± 1.0	1.1	0.752
	50-74	2.4 ± 0.5	± 1.0	4.8	0.621
	75-99	6.0 ± 0.6	± 1.2	10.0	0.408
	100	8.1 ± 1.2	± 2.5	6.8	0.653
Deep	1-24	1.6 ± 0.4	± 0.9	4.0	<0.001
	25-49	1.1 ± 0.4	± 0.8	2.1	0.240
	50-74	4.9 ± 0.5	± 1.0	9.8	0.002
	75-99	6.5 ± 0.6	± 1.2	1.8	0.113
	100	1.3 ± 1.2	± 2.5	1.0	0.004
Random Effects		sd			
Plot:(Fence:Block)		0.5			
Fence:Block		0.0			
Block		0.7			

Table 7: Effects of snow-depth treatments (fixed effect) on the snow melt date (day of year) in the "all treatments" and "all years" datasets for all species fitted with a linear mixed effects model.

Snowmelt Date	Year	Effect ± se	Confidence Interval	t-value	p-value
All Treatments					
Fixed Effects					
Ambient (Intercept)	2010	142.8 ± 0.9	± 1.7	158.7	<0.001
	2011	12.1 ± 0.9	± 1.7	13.5	0.211
	2012	14.9 ± 0.9	± 1.7	16.5	<0.001
	2013	8.0 ± 0.9	± 1.7	8.9	0.037
Shallow	2010	-10.5 ± 1.0	± 2.0	-10.5	<0.001
	2011	6.7 ± 1.0	± 2.0	6.7	0.123
	2012	7.4 ± 1.0	± 2.0	7.4	0.035
	2013	4.4 ± 1.0	± 2.0	8.9	0.002
Medium	2010	18.4 ± 0.9	± 1.8	20.5	<0.001
	2011	20.1 ± 1.0	± 1.9	20.1	0.992
	2012	25.6 ± 1.0	± 1.9	25.6	0.281
	2013	-15.8 ± 1.0	± 1.9	-15.8	0.001
Deep	2010	25.8 ± 0.9	± 1.7	28.7	<0.001
	2011	22.6 ± 0.9	± 1.7	25.2	0.004
	2012	29.3 ± 0.9	± 1.7	32.5	0.002
	2013	19.4 ± 0.9	± 1.7	21.6	<0.001
Random Effects		sd			
Plot:(Fence:Block)		2.4			
Fence:Block		1.1			
Block		3.8			
All Years					
Fixed Effects					
Ambient (Intercept)	2008	158.6 ± 1.2	± 2.3	132.2	<0.001
	2009	-5.8 ± 1.1	± 2.3	-5.3	0.040
	2010	-15.9 ± 1.2	± 2.3	-13.2	<0.001
	2011	-3.8 ± 1.2	± 2.3	-3.1	<0.001
	2012	-1.1 ± 1.2	± 2.3	-0.9	<0.001
	2013	-7.8 ± 1.2	± 2.3	-6.5	<0.001
Deep	2008	16.0 ± 1.2	± 2.3	13.3	<0.001
	2009	11.0 ± 1.2	± 2.3	9.2	0.040
	2010	10.3 ± 1.2	± 2.3	8.6	<0.001
	2011	6.6 ± 1.2	± 2.3	5.5	<0.001
	2012	13.4 ± 1.2	± 2.3	11.2	<0.001
	2013	3.4 ± 1.2	± 2.4	2.8	<0.001
Random Effects		sd			
Plot:(Fence:Block)		2.9			
Fence:Block		2.7			
Block		1.5			

Table 8: Effects of snow-depth treatments (fixed effect) on the season length (number of days) in the "all treatments" and "all years" datasets for all species fitted with a linear mixed effects model.

Senescence Length	**Year**	**Effect ± se**	**Confidence Interval**	**t-value**	**p-value**
All Treatments					
Fixed Effects					
Ambient (Intercept)	2010	86.0 ± 2.4	± 4.8	3.6	<0.001
	2011	-10.9 ± 2.4	± 4.8	-4.6	0.211
	2012	-8.0 ± 2.3	± 4.7	-3.4	<0.001
	2013	-5.8 ± 2.4	± 4.8	-2.4	0.037
Shallow	2010	4.3 ± 2.4	± 4.9	1.8	<0.001
	2011	-9.2 ± 2.5	± 5.1	-3.7	0.123
	2012	-3.6 ± 2.5	± 5.1	-1.4	0.035
	2013	-3.0 ± 2.6	± 5.3	-1.2	0.002
Medium	2010	-10.9 ± 2.4	± 4.8	-4.5	<0.001
	2011	-11.3 ± 2.5	± 5.0	-4.5	0.992
	2012	-12.6 ± 2.5	± 5.0	-5.0	0.281
	2013	-6.0 ± 2.6	± 5.1	-2.3	<0.001
Deep	2010	-12.3 ± 2.4	± 4.8	-5.1	<0.001
	2011	-11.2 ± 2.4	± 4.9	-4.7	0.004
	2012	-12.1 ± 2.4	± 4.7	-5.0	0.002
	2013	-10.7 ± 2.5	± 4.9	-4.3	<0.001
Random Effects		sd			
Plot:(Fence:Block)		2.4			
Fence:Block		2.2			
Block		4.3			
All Years					
Fixed Effects					
Ambient (Intercept)	2008	70.0 ± 2.2	± 4.3	31.8	<0.001
	2009	5.6 ± 2.1	± 4.2	2.7	0.704
	2010	16.1 ± 2.1	± 4.2	7.7	0.708
	2011	5.2 ± 2.2	± 4.3	2.4	0.138
	2012	8.1 ± 2.1	± 4.2	3.9	<0.001
	2013	10.3 ± 2.2	± 4.3	4.7	0.015
Deep	2008	-9.9 ± 2.2	± 4.3	-4.5	<0.001
	2009	-0.8 ± 2.1	± 4.2	-0.4	0.001
	2010	3.7 ± 2.1	± 4.3	1.7	<0.001
	2011	4.6 ± 2.2	± 4.3	2.1	0.015
	2012	3.9 ± 2.1	± 4.2	1.9	0.002
	2013	5.0 ± 2.2	± 4.4	2.3	0.646
Random Effects		sd			
Plot:(Fence:Block)		2.0			
Fence:Block		3.1			
Block		3.6			

Appendix A – Maps and Photos

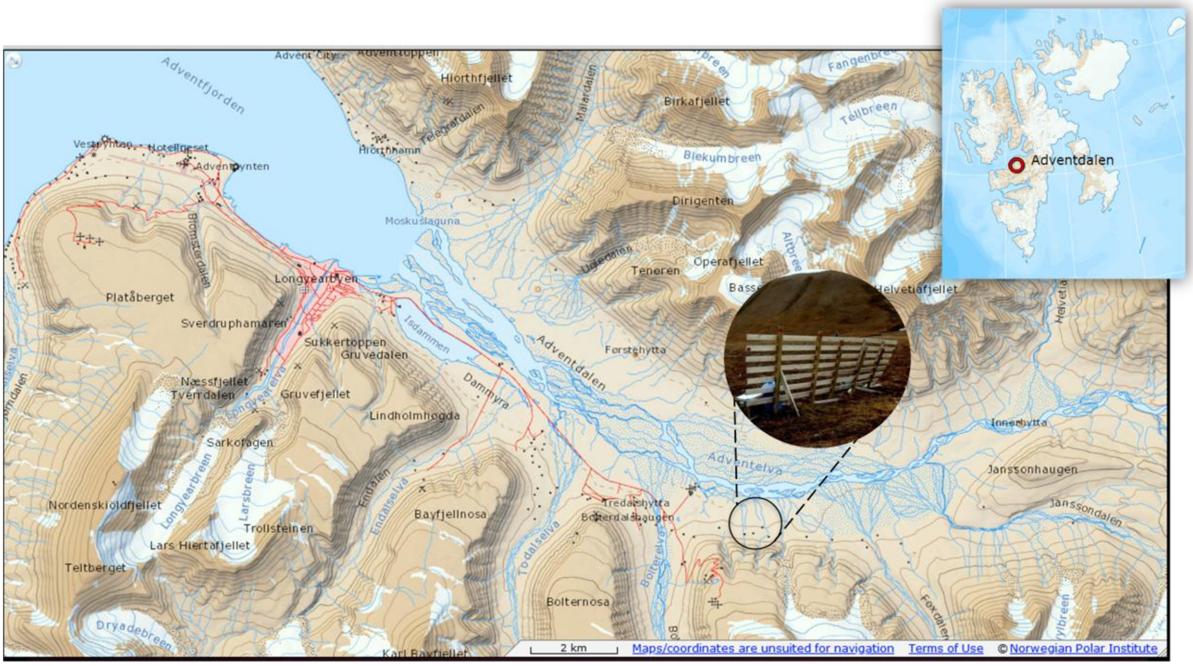

Figure 11: The field site was located in Adventdalen (78°17´N, 16°07´E) in a glacial valley located 12 km east of Longyearbyen in Spitsbergen, Svalbard (toposvalbard.npolar.no).

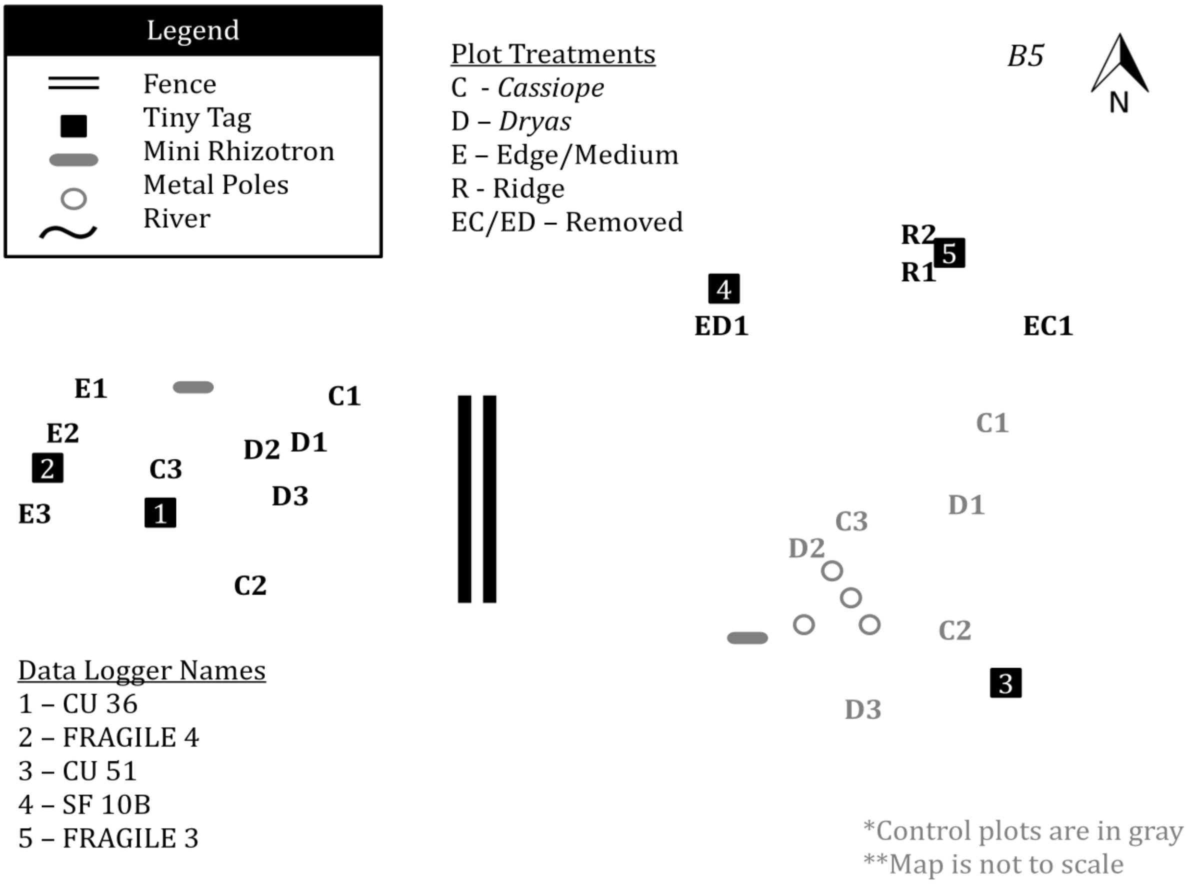

Figure 12: Site layout of one of the twelve snow fences in Adventdalen, Svalbard.

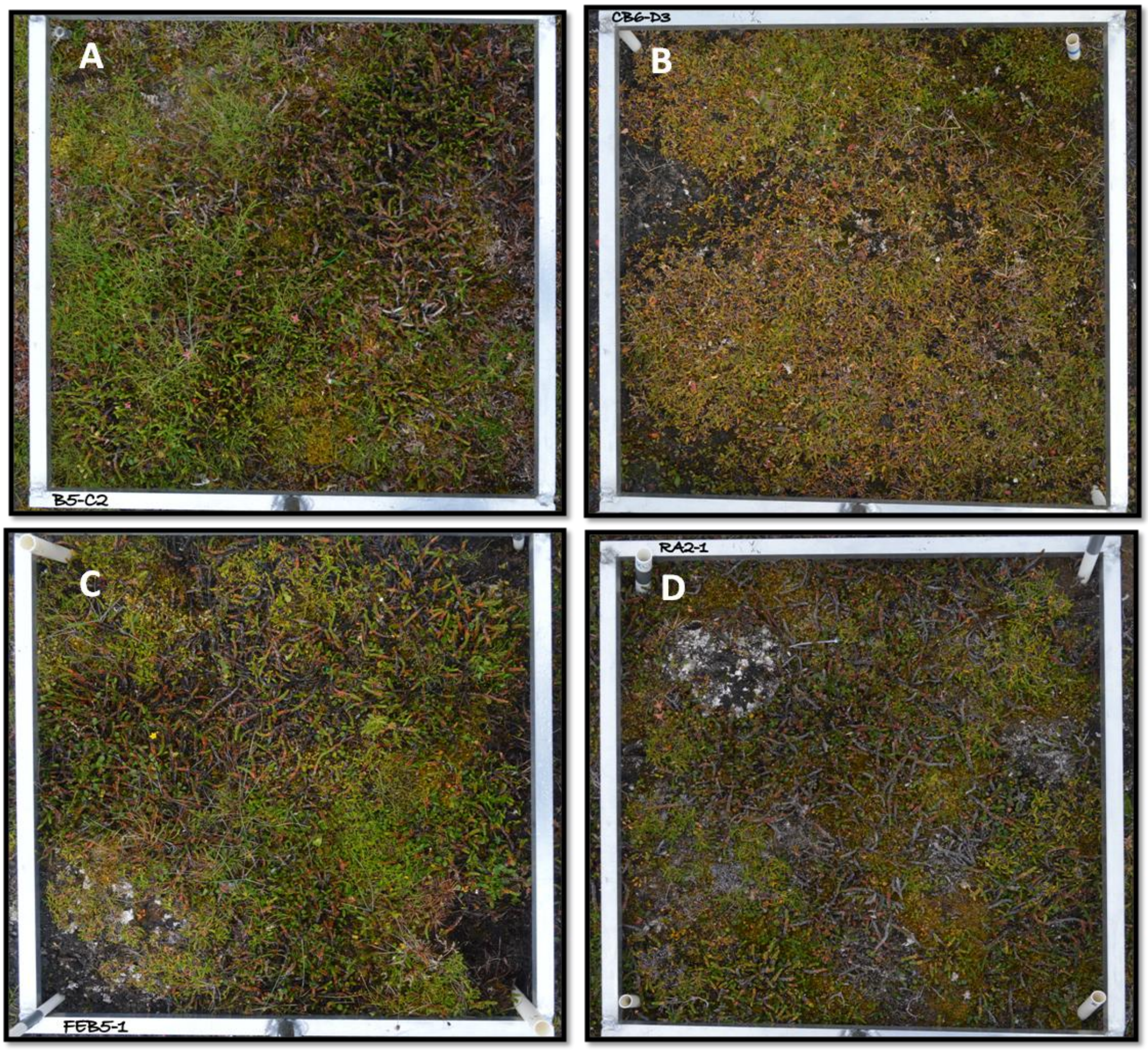

Figure 13: Example of a plot from each snow treatment (a) deep, (b) ambient, (c) medium, and (d) shallow at the start of the sampling period in 2013 at the snow fence site in Adventdalen, Svalbard.

Figure 14: Autumn leaf senescence gradient (a) 1-24%, (b) 25-49%, (c) 50-74%, (d) 75-99%, of *Pedicularis hirsuta* in Adventdalen, Svalbard.

Appendix B - Supplementary Information

Climate change and snow in the Arctic

Temperature and precipitation are predicted to increase over the next 100 years in the Arctic, and understanding how these changes are expected to impact tundra communities is critical for future management of the Arctic region. Due to polar amplification, the Arctic (67.5°N to 90°N) is expected to warm between 2.2 to 2.4 times more per year than the global average warming temperature for 2081-2100 using the CMIP5 model (Coupled Model Intercomparison Project Phase 5); with the greatest effect in the early winter months (Collins *et al*. 2013). Using the CCSM4 model (Community Climate System Model, version 4) the autumn season in the Arctic will be impacted the most by climate change, with November and October being the most responsive to changes in temperature, precipitation, cloud cover, air pressure and sea ice concentration (Vavrus *et al*. 2012).

Increasing temperatures in tundra communities was found in a meta-analysis to positively affect canopy height, maximum height of growth forms, the abundance of shrubs and dead material, and negatively affect the abundance of lichens and moss, although these effects are highly site-specific (Elmendorf *et al*. 2012). Potential impacts of increased snow cover were a warmer soil surface during the winter, since snow acts as a thermal insulator and heat-loss was reduced maintaining warmer soil temperatures (Hinkel *et al*. 2003). Under simulated climate warming, vegetative and reproductive development in *Dryas* occurred earlier in the growing season (Welker *et al*. 1997). Alpine areas where shrubs were abundant reacted differently to increased snow cover, since productivity is dependent on summer moisture availability and a longer growing season (Billings & Bliss 1959). Trees and shrubs accumulated snow in the branches and naturally acted like a snow fence resulting in warmer soil temperatures in the winter promoting microbial activity and respiration; further encouraging shrub encroachment. Snow cover was greatly affected by shrub canopies;

however, in contrast to the fences, spring melt-out will be earlier as a result of the low albedo around visible branches (Myers-Smith *et al*. 2011). Snow cover in the Arctic is primarily distributed by strong wind currents and topography, displacing snow onto the sides of ridges and gullies (Billings & Bliss 1959). Areas with thinner snow cover, such as ridges and slopes melt-out earliest (Billings & Bliss 1959) and as seen in the shallow plots at the snow fences in Adventdalen (Fig. 2).

Senescence

Leaf senescence has been well-studied in agricultural and botanical settings. Drought-induced stress can cause pre-mature leaf senescence in *Salvia officinalis* which is followed by a change in phytohormones, such as an increase in salicylic acid and a decrease in jasmonic acid (Abreu & Munné-Bosch 2008). In spring wheat (*Triticum aestivum*) and two wheat cultivars, ozone (O_3) decreased the chloroplast size and accelerated leaf senescence (Ojanperä *et al*. 1997; Burkart *et al*. 2013). In contrast, O_3 did not impact the timing of senescence in five meadow species in Finland, but did alter reproduction and fruit size (Rämö *et al*. 2007). Ozone exposure in two of four tree species accelerated senescence-related nutrient processes; however, species specificity to ozone may be related the chlorophyll levels in the leaves and spongy parenchyma thickness (Ribas *et al*. 2005). Ghanem *et al*. (2008) observed phytohormonal changes during leaf senescence in tomato plants (*Solanum lycopersicum*) subjected to high concentrations of Na^+ of which an ethylene precursor was responsible for the onset of senescence and the decrease in chlorophyll.

Genetically, leaf senescence is a highly regulated process that consists of positive and negative regulatory elements that control the precise timing of senescence; and can be influenced by plant development, such as growth and leaf formation (Lim *et al*. 2007). Developmental leaf senescence cues differ from environmentally induced senescence in the early phases; however, similar genes (senescence-associated genes) were shared during the yellowing and later phases (Guo & Gan 2012). Antioxidants and redox factors largely influence senescence, although reactive oxygen species generation respond the earliest (Khanna-Chopra 2012). Senescence was characterized by four anti-oxidants (1) catalase, (2) peroxidase, (3) ascorbate peroxidase and, (4) superoxide dismutase which increase and decrease during the different stages of senescence; and the concentrations of each varied per species, in gingko and birch (Kukavica & Jovanovic 2004). Arrom & Munné-Bosch (2012) found that abscisic acid (ABA) increased in *Lilium* sp. during senescence and that darkness promoted the build-up of ABA levels. Future studies of ABA in Arctic plants, may provide insight into the effects of day-length on senescence. Lev-Yadun *et al*. (2012) found that spring and fall leaf coloration may be caused by both plant physiology and plant-herbivore interactions. Timing of leaf senescence may also affect summer grazers, such as geese and reindeer. Lesser snow geese in Northern Canada were able to detect carbohydrate rich shoots (Jefferies & Edwards 2008). Few studies have been done on *Alopecurus* though it is an important food source for grazing geese. A study in 2006 found that *Alopecurus magellanicus* (syn. *borealis*) was common in mesic habitats, and its growth rate increased when inside open-top chambers (Cooper *et al*. 2006). In the autumn, plant productivity and soluble carbohydrates decreased as senescence was reached, thus early senescence may be problematic for forage species (Jefferies & Edwards 2008).

Appendix C - Additional Figures

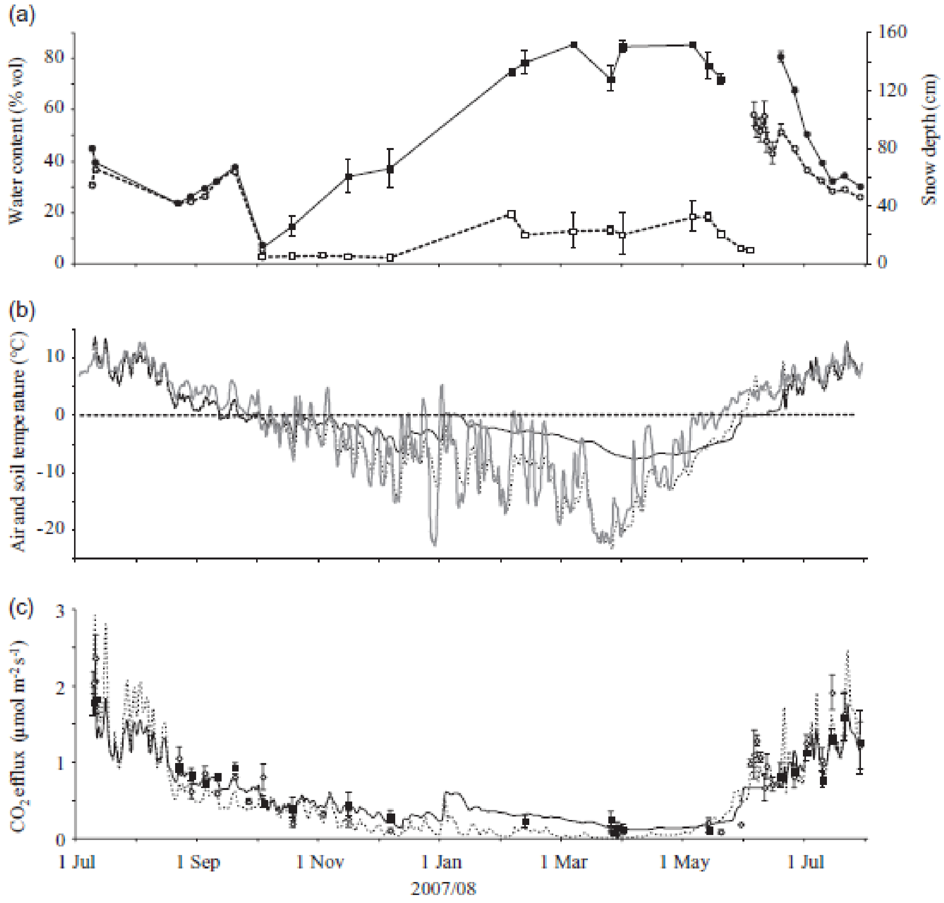

Figure 15: Water content, air and soil temperature, and CO_2 efflux in a meadow habitat at the snow fence experiment in Adventdalen, Svalbard in 2007/8 beginning in July. For more details see Morgner *et al*. (2010).

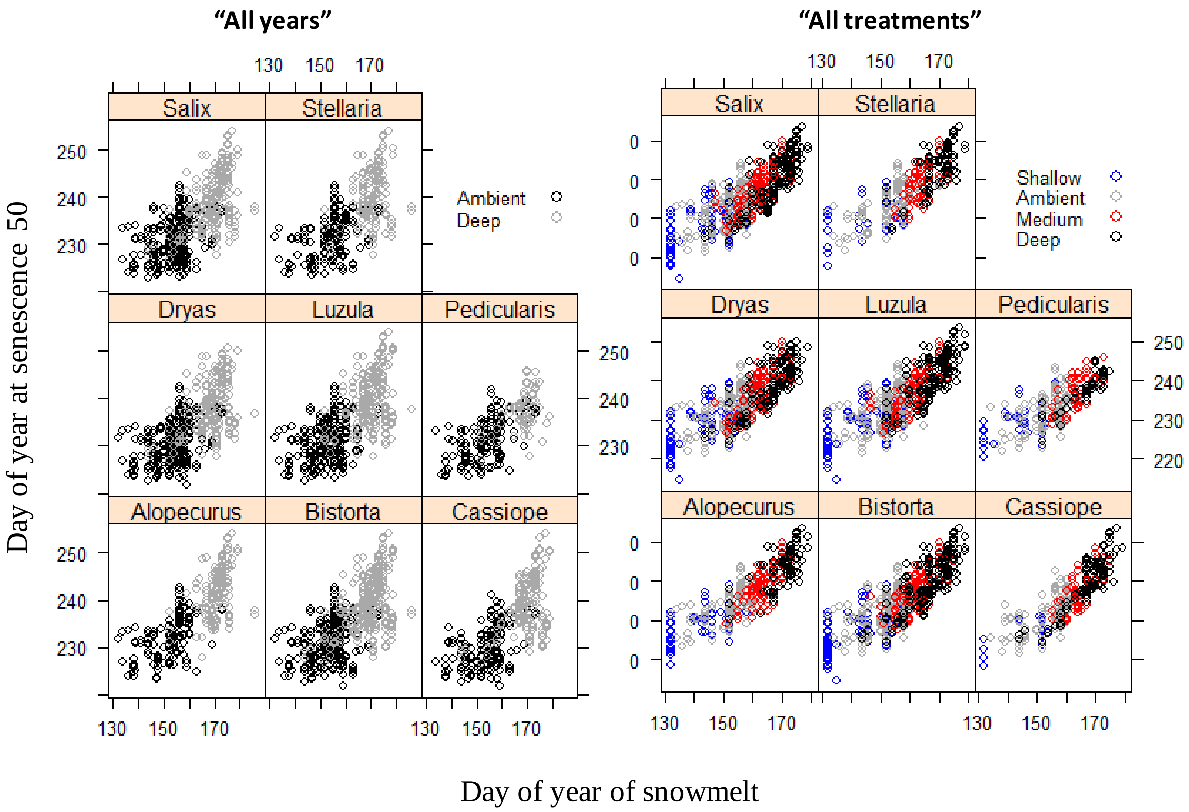

Figure 16: Relationship between the day of year to reach senescence 50 (50-74% senesced leaves) with snowmelt for the "all years" and "all treatments" datasets for each species, *Alopecurus magellanicus*, *Bistorta vivipara*, *Cassiope tetragona*, *Dryas octopetala*, *Luzula confusa*, *Pedicularis hirsuta*, *Salix polaris*, and *Stellaria longipes*.

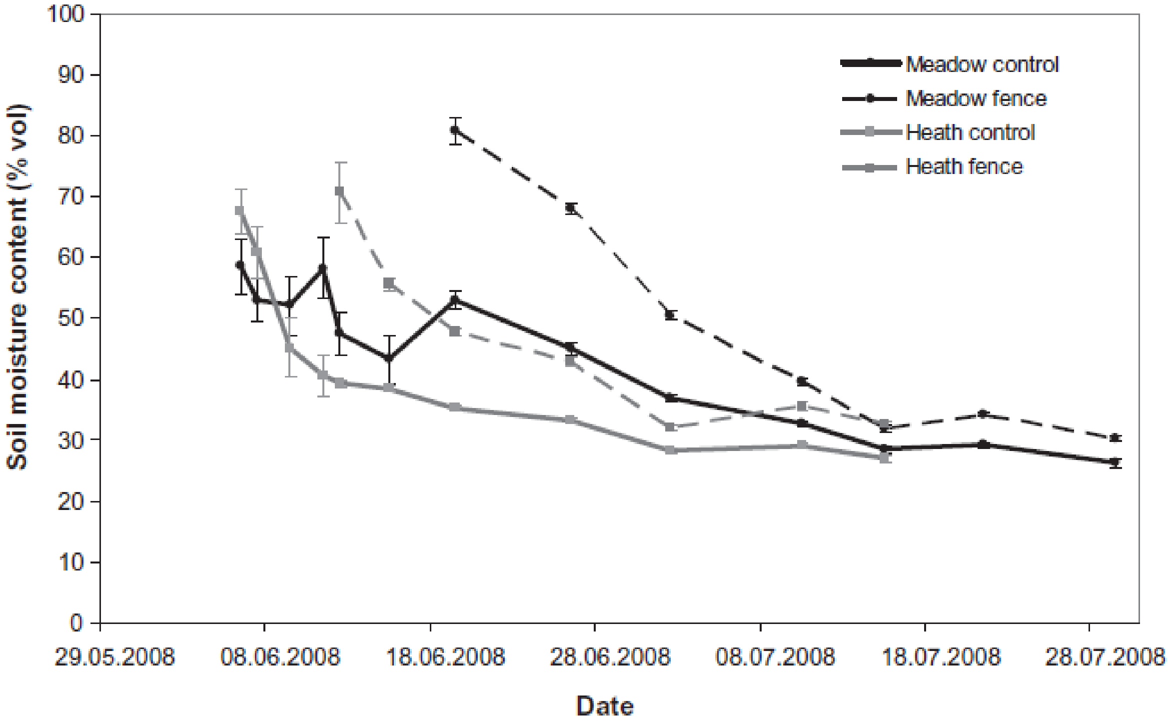

Figure 17: Soil moisture content at the deep snow-depth treatment from the snow fence experiment in Adventdalen, Svalbard from May 29th – July 28th, 2008. For more details, see Cooper *et al*. (2011).

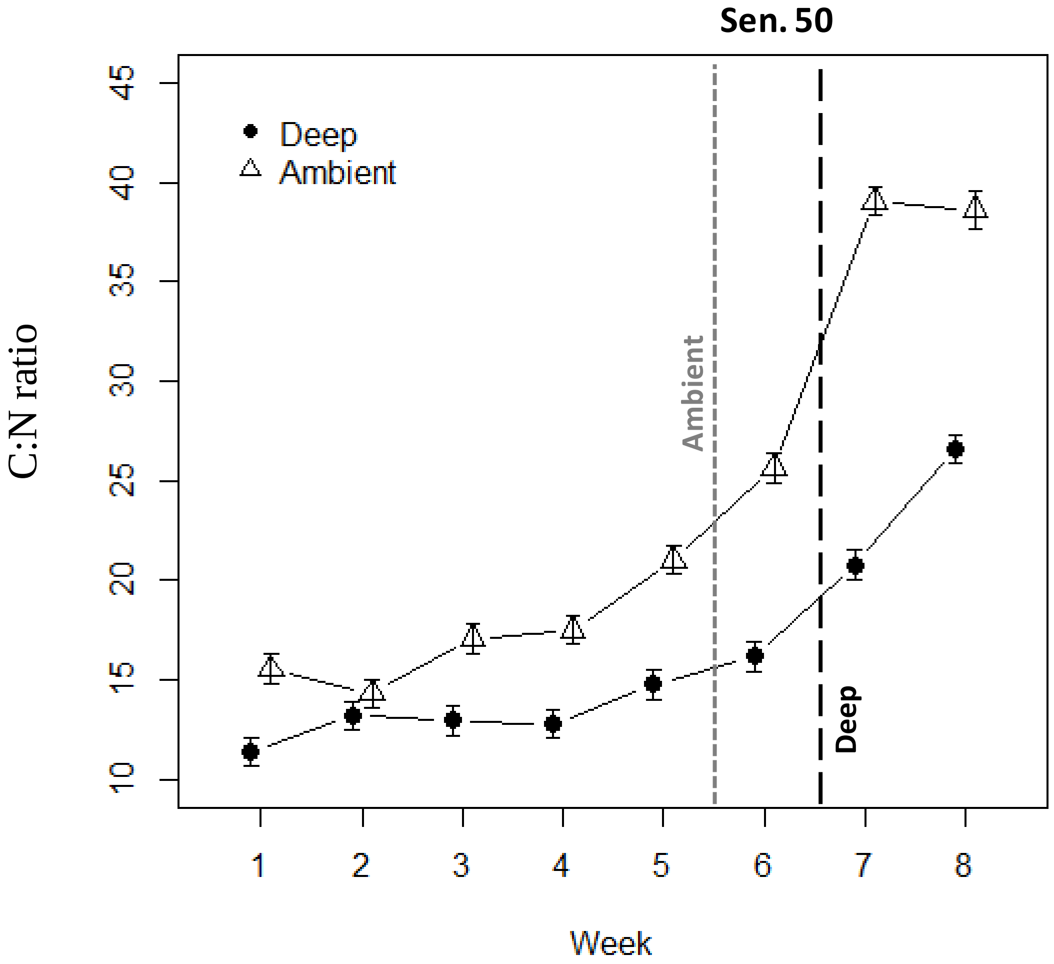

Figure 18: Carbon to nitrogen ratio in the soil (effect size ± se) in *Salix* plots of two snow-depth treatments (ambient, deep) on July 20th – September 14th, 2012. Dashed lines indicate the timing of senescence 50 for each treatment.

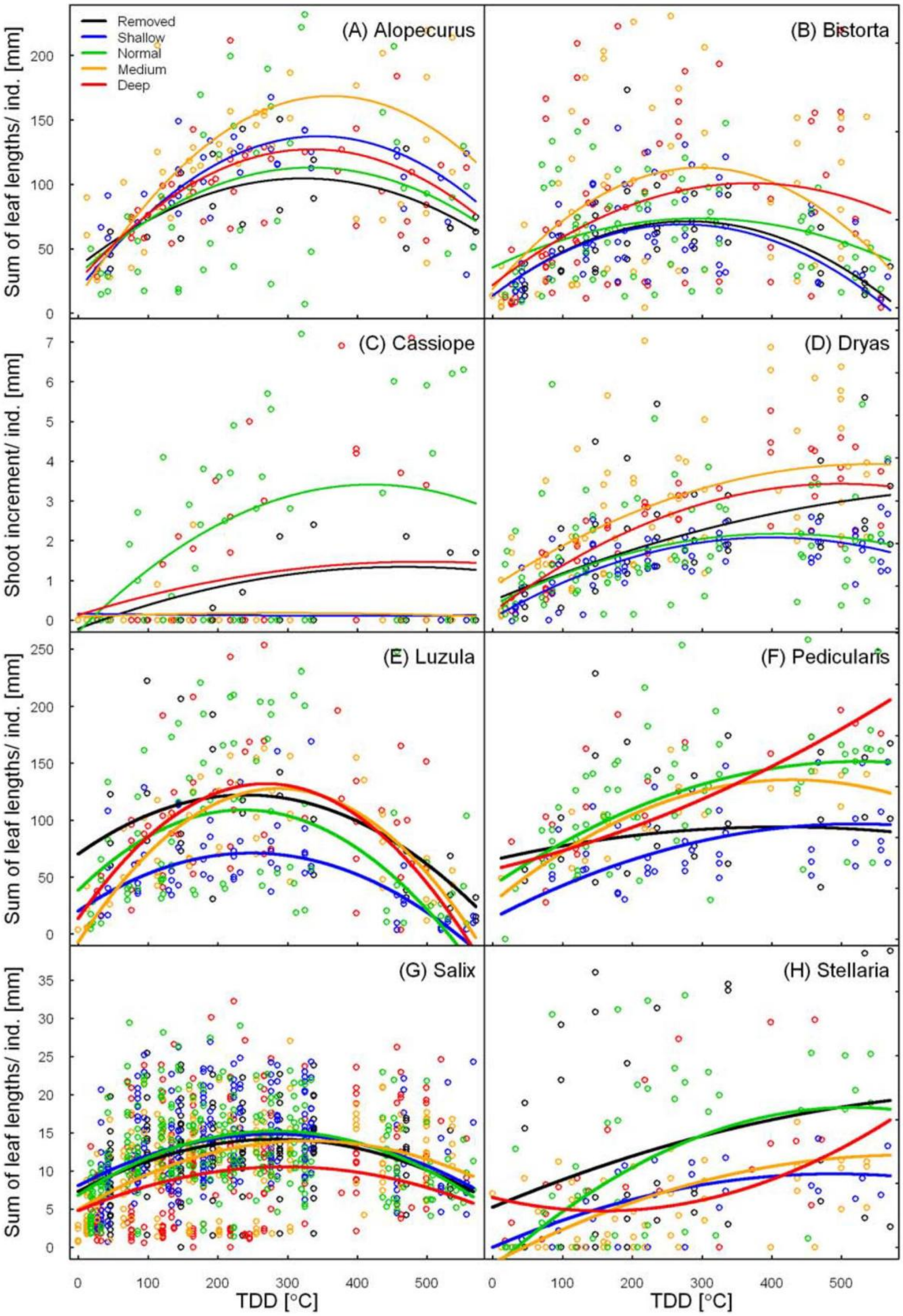

Figure 19: Relationship between the thawing degree days (TDD) with plant characteristics in eight species at the snow fence experiment in Adventdalen, Svalbard during the summer of 2012. For more details, see Rumpf *et al*. (2014).

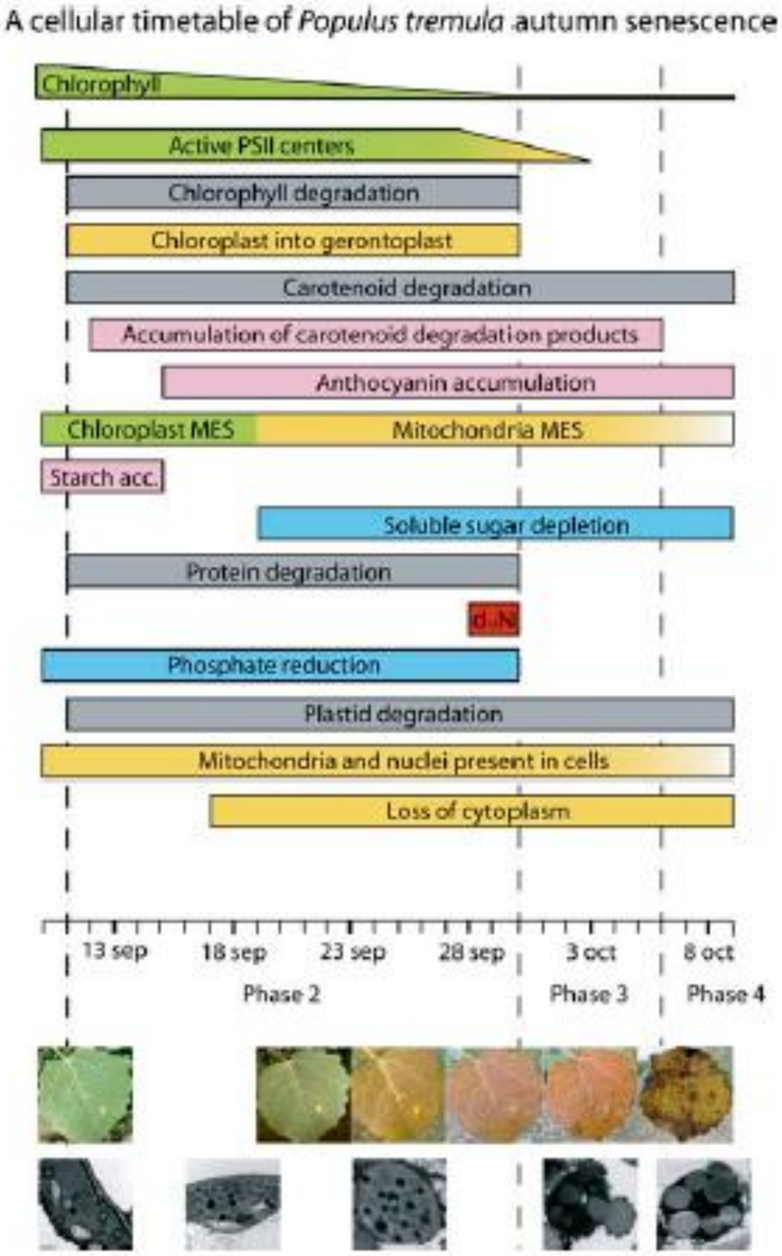

Figure 20: Cellular timetable of the senescence phases in *Populus tremula*. See more details in Keskitalo *et al*. (2005).

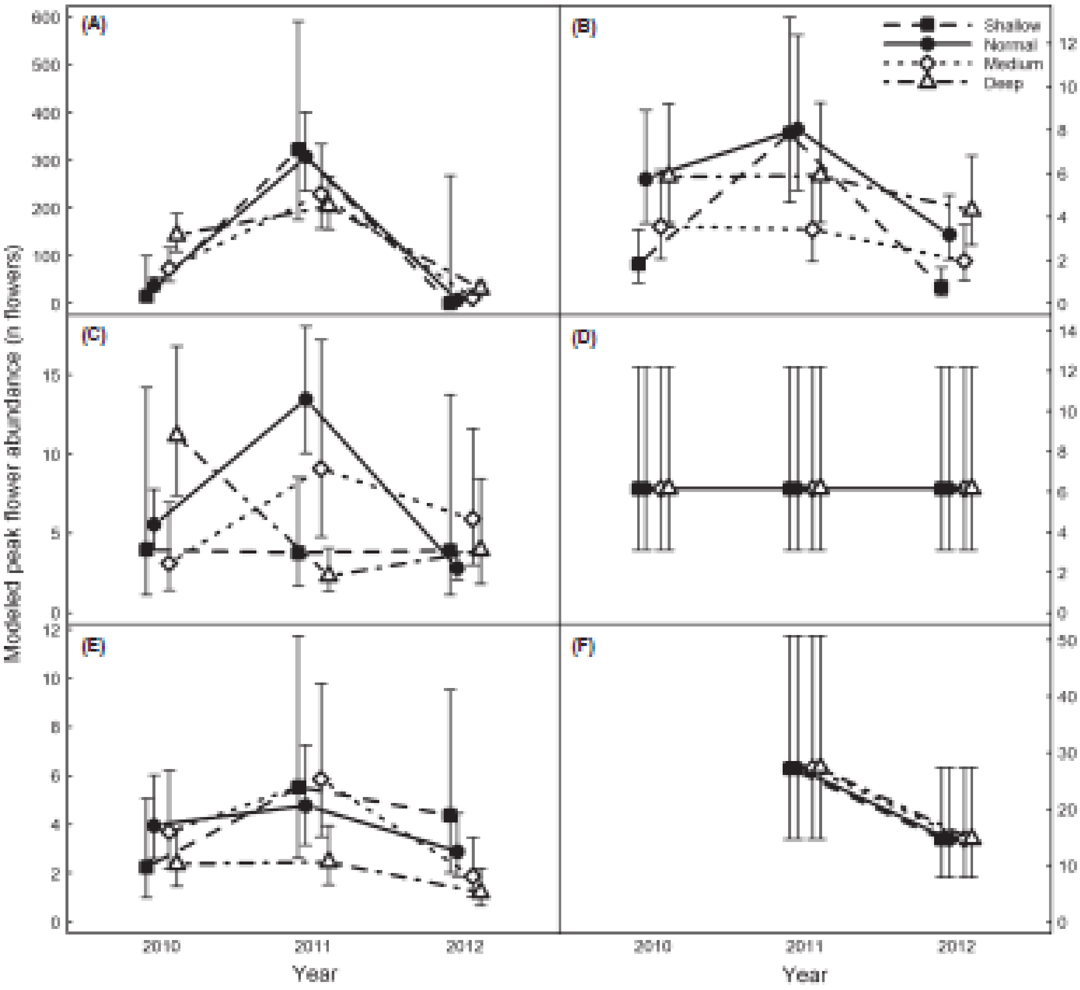

Figure 21: Flower abundance of six species, (a) *Cassiope tetragona*, (b) *Dryas octopetala*, (c) *Pedicularis hirsuta*, (d) *Saxifraga oppositifolia*, (e) *Stellaria longipes* (syn. *crassipes*), and (f) *Bistorta vivipara* subjected to four snow-depth treatments (shallow, normal, medium, deep) at the snow fence experiment in Adventdalen, Svalbard in the summer of 2010-2012. See more details in Semenchuk *et al*. (2013).

Appendix D – R Scripts

Example of the timing of senescence 50 using the all years dataset

```
library(lme4)
require("Hmisc")
dat$year<-factor(dat$year)
dat$treat <- factor(dat$treat, levels=c("cont","incr"))
dat$treat <- relevel(dat$treat, ref="cont")
model<-lmer(doy~treat*year +(1|block/fence/plot), data=na.omit(dat))
print(model)

fm1=model
new.data=with(na.omit(dat), expand.grid(treat=unique(treat),year=unique(year),doy=0))
mm <- model.matrix(terms(fm1),new.data)
new.data$distance <- mm %*% fixef(fm1)
pvar1 <- diag(mm %*% tcrossprod(vcov(fm1),mm))
new.data <- data.frame(
   new.data
   , plo = new.data$distance-1*sqrt(pvar1)
   , phi = new.data$distance+1*sqrt(pvar1)
)

fac <- factor(new.data$year, levels=c("8", "9", "10", "11","12", "13"))
new.data$year2= as.numeric(levels(fac))[fac]
new.data3=rbind(new.data[3:6,],new.data[1:2,],new.data[7:8,],new.data[11:12,],new.data[9:10,])
new.data1=subset(new.data3,treat=="cont")
new.data2=subset(new.data3,treat=="incr")
errbar(new.data1$year2, new.data1$distance, new.data1$plo,new.data1$phi,xlab="Year", ylab=" Day of Year", type="b",pch=2, col="black", errbar.col="black",lwd=0.5, cex=1.3, ylim=c(225,255))
errbar(new.data2$year2, new.data2$distance, new.data2$plo, new.data2$phi, type="b", col="black",cex=1.3, errbar.col="black",lwd=0.5, add=TRUE)# final lines
legend("topleft", inset=.05, c("Deep","Ambient"), pch=c(16,2), bty="n")

library(lmerTest)

(model<-lmer(doy~treat*year +(1|block/fence/plot), data=na.omit(dat)))
anova(model, ddf="lme4")
summary(model)
```